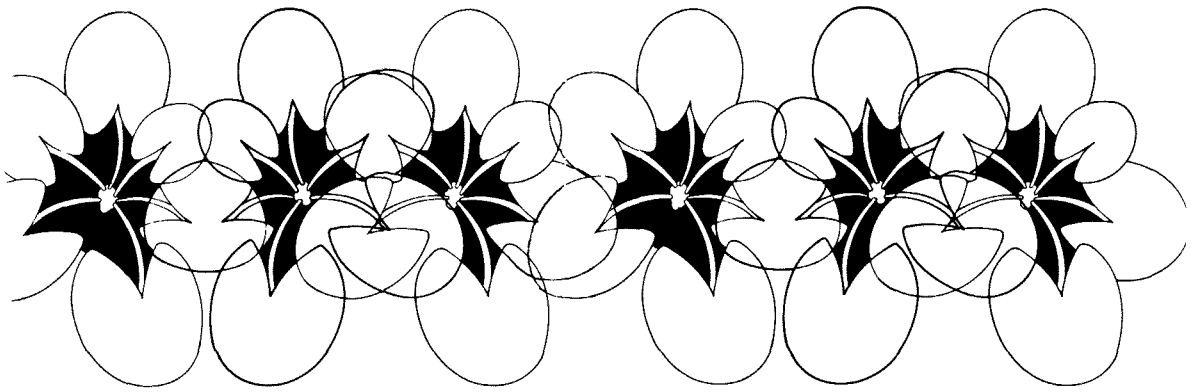
ECOLOGICAL STUDIES ON NYMPHAEID WATER PLANTS



Theo C.M. Brock

ECOLOGICAL STUDIES ON NYMPHAEID WATER PLANTS

with emphasis on production and decomposition

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PROEFSCHRIFT

ter verkrijging van de graad van
doctor in de Wiskunde en Natuurwetenschappen
aan de Katholieke Universiteit te Nijmegen,
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Prof Dr J H.G.I. Giesbers
volgens besluit van het College van Dekanen
in het openbaar te verdedigen
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Theodorus Cornelis Maria Brock

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PROMOTOR

Prof. Dr. C. den Hartog

CO-REFERENT

Dr. G. van der Velde

CONTENTS

Dat alleen mijn naam op de omslag van dit proefschrift prijkt, verdient gerelativeerd te worden. Zonder het vertrouwen en de hulp van vele anderen zou dit werkstuk niet tot stand gekomen zijn.

Allereerst wil ik mijn ouders bedanken. Vooral zij hebben door hun levenswijze en hun betrokkenheid met de natuur mijn interesse voor de biologie aangewakkerd. Zij hebben me ook doen beseffen dat kennis zonder betrokkenheid geen waarde heeft.

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De afdeling Aquatische Oecologie is een uitstekende leerschool geweest, waar ik mijn onderzoeks- en onderwijsvaardigheden heb kunnen ontplooien. De sfeer en kameraadschap die ik daar heb gekend hebben een belangrijke rol gespeeld bij het wordingsproces van dit proefschrift. Beste (ex-)collega's, ik hoop jullie niet uit het oog te verliezen.

Het kritisch commentaar op eerdere versies van onderdelen van dit proefscrift, dat ik heb mogen ontvangen van mijn promotor, co-referent, Ron Phillips, Hannie Geelen, Eddy Delbecque, Dolf van Wijk, Francien Heijs, Joop Brouns en Jaap Boon zijn van onschatbare waarde geweest. Ook Jan Klerkx ben ik veel dank verschuldigd voor de talrijke suggesties die hij gedaan heeft om de engelse tekst te verbeteren. Ik besef dat ik soms lastig en eigenwijs was door uitvoerig tekst en uitleg op de kritiek te vragen.

De tekeningen en grafieken in dit proefschrift zijn een onmisbaar deel van het geheel. Hiervoor ben ik de medewerkers van de afdelingen Illustratie, Fotografie en Reproductie zeer erkentelijk. Mijn speciale dank gaat uit naar de heer J.J.A. Slippens voor het ontwerp van de omslag.

Hoewel de naam anders doet vermoeden deed de auto-analyser zijn werk niet zonder hulp van de heer L.M.P.J. Meuffels. Beste Leo, bedankt voor het draaiende houden van dat apparaat waardoor een schat aan gegevens beschikbaar is gekomen.

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Aan jullie allen wil ik dit proefschrift opdragen.

SCOPE OF THE RESEARCH PROJECT

Relatively small and shallow aquatic ecosystems, whether natural (e.g. oxbow lakes, moorland pools) or man-made (e.g. ditches, canals), are characteristic elements of the Dutch landscape. Many of these systems are, at least potentially, dominated by aquatic vascular plants. Recently the literature on these plants and their communities has been expanding rapidly and in general terms their roles and requirements are fairly well understood. However, more specific knowledge on the ecology of most hydrophyte communities is fragmentary. A more or less complete model of the structure, functioning and dynamics of some common hydrophyte communities would definitely be of importance in that it would offer a better insight in the effects of human interference on shallow aquatic ecosystems and would help to develop an adequate management and conservancy policy.

In 1973, the Laboratory of Aquatic Ecology (Catholic University of Nijmegen, The Netherlands) started with a research project on the ecology of aquatic macrophytes and macrophyte-dominated systems (Den Hartog, 1976; 1978; 1983). Within the framework of this project a survey has been made of the distribution of aquatic macrophytes in The Netherlands, in relation to several physico-chemical parameters of the overlying water and the bottom compartments (see e.g. Roelofs, 1983; Roelofs et al., 1984). Apart from these investigations intensive surveys have been carried out of the structure, functioning and dynamics of some selected hydrophyte communities in marine (e.g. Jacobs, 1982; Brouns, 1985; Heijs ,1984), brackish-water (e.g. Verhoeven, 1980; Van Vierssen, 1982; Van Wijk, 1983) and freshwater ecosystems (Van der Velde, 1980) in The Netherlands and abroad.

In the freshwater environment work has concentrated on communities dominated by nymphaeids. Aquatic vascular plants with a nymphaeid growth form fill up the available space in a characteristic way. Most of their photosynthetic tissues float at the surface of the water. They possess a well-developed root system. The leaf-blades at the water surface and the underground plant parts are connected by long slender petioles.

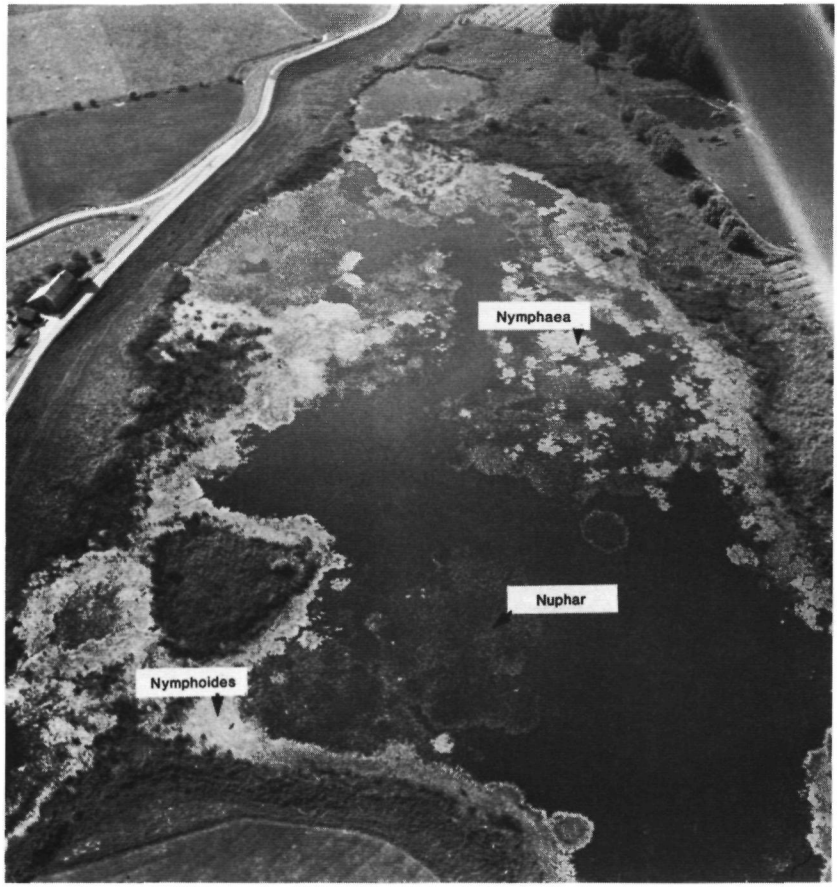

Figure 1: Aerophotograph of the Oude Waal in the summer of 1975, showing dense stands of *Nuphar lutea, Nymphaea alba* and *Nymphoides peltata*.

Structurally, nymphaeids can be regarded as more or less intermediate between emergent and submerged aquatic macrophytes (Van der Velde, 1980). Communities dominated by nymphaeids are a suitable object for an intensive research programme because;

a) they are common in shallow fresh waters all over the world,
b) they often form characteristic belts and stages within the zonation and succession sequences of hydrophyte communities,
c) many shallow (< 3m) fresh waters in The Netherlands are dominated by nymphaeid water plants (see e.g. Figure 1),

d) in general, nymphaeids have received less attention than emergent and submerged macrophytes, and,
e) communities dominated by nymphaeids are rather complex, since they consist of a large number of structural elements (see e.g. Van der Velde, 1980).

Some characteristic nymphaeids which can dominate hydrophyte communities in The Netherlands, and which are studied within the context of this research project, are *Nuphar lutea* (L.)Sm., *Nymphaea alba* L., *Nymphaea candida* Presl and *Nymphoides peltata* (Gmel.)O.Kuntze. At present a research team is unraveling the structure, functioning and dynamics of the nymphaeid system.

Several case studies on the nymphaeid system have been published lately. In nymphaeid-dominated communities the macrophytes can be considered to constitute the basic framework of the system. Hence, several studies have dealt with the nymphaeids themselves, e.g. their geographical distribution in The Netherlands (Giesen and Van der Velde, 1978), their floral biology and seed production (Van der Velde et al., 1978; Van der Velde and Van der Heijden, 1981; Giesen and Van der Velde, 1983) and the development and initial decomposition of their floating leaves (Lammens and Van der Velde, 1978; Van der Velde et al., 1982; Van der Velde and Peelen-Bexkens, 1983; Van der Velde and Van der Heijden, 1985). Other papers have reported about the organisms associated with the system, such as semi-aquatic and aquatic macro-invertebrates (Van der Velde, 1978; Van der Velde and Brock, 1980; Brock and Van der Velde, 1983), periphytic diatoms and multicellular-algae (Delbecque, 1983; Delbecque and Chatrou, 1983; Delbecque, 1985) and phytoplankton (Roijackers, 1983, 1984). Most of the field studies were carried out in the Oude Waal and Bemmelse Strang, two alkaline oxbow lakes of the river Waal near Nijmegen (Figure 2). Some of the studies were performed in several aquatic ecosystems (e.g. apart from the Oude Waal and Bemmelse Strang also in the Haarsteegse Wiel near Vlijmen, the Voorste Choorven near Oisterwijk and the Grote Vilt near Beugen). The underlying assumption is that by studying several aspects of the nymphaeid system, it should be possible, through integration of the various case studies, to arrive at a more or less complete structural and functional model of a macrophyte-dominated system in the freshwater environment (Den Hartog, 1983). At the moment this model is not yet complete. Several publications are in preparation which attempt to describe in greater detail the distribution of nymphaeids in

relation to physico-chemical parameters, the effects of the nymphaeid vegetation on phyto- and zooplankton , and the structure of the nymphaeid-associated epiphyte and invertebrate communities. In 1984, a study of the germination and seedling ecology of nymphaeids was initiated by mr. A.J.M. Smits.

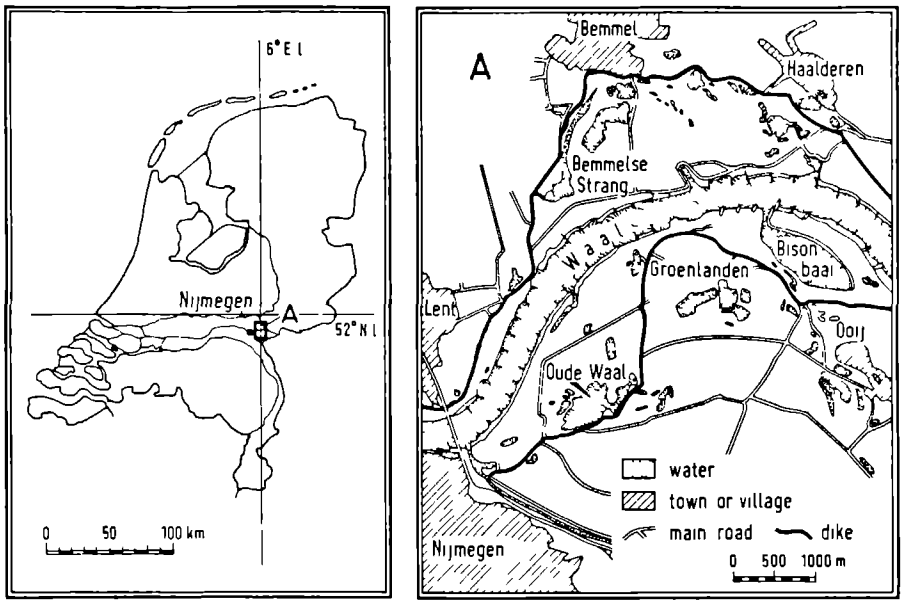

Figure 2: The location of the Oude Waal and Bemmelse Strang in the forelands of the river Waal near Nijmegen.

The studies described in the present thesis also aim at making a contribution to a better understanding of the nymphaeid system. Before presenting 5 case studies on some functional aspects of *Nuphar lutea, Nymphaea alba* and *Nymphoides peltata*, a general description will be given of the distribution and survival biology of these nymphaeids (chapter 2). In chapters 3, 4, and 5, aspects of biomass production, nutrient cycling and decomposition of *Nymphoides peltata* are presented. The principal objective of the research on *Nymphoides peltata* was to get a more or less detailed picture of the functioning of a nymphaeid water plant in the oxbow lake environment. Another objective was to gain some insight into the decomposition of the different nymphaeid macrophytes and the environmental factors which influence the decomposition in nature. For this reason, research on various aspects of decomposition of *Nuphar lutea*

(Chapter 6) and *Nymphaea alba* (chapter 7) is presented as well. In chapter 8 a synthesis will be given of the present knowledge concerning the role of nymphaeids in their ecosystem.

References

Brock, Th.C.M. and Van der Velde, G., 1983. An autecological study on *Hydromyza livens* (Fabricius) (Diptera, Scatomyzidae), a fly associated with nymphaeid vegetation dominated by *Nuphar*. Tijdschr. Ent., 126:59-90.

Brouns, J.J.W.M., 1985. The plastochrone interval method for the study of the productivity of seagrasses. Possibilities and limitations. Aquat. Bot., 21:71-88.

Delbecque, E.J.P., 1983. A comparison of the periphyton of *Nuphar lutea* and *Nymphaea alba*. In: Wetzel, R.G. (ed.), Periphyton of freshwater ecosystems. Developments in Hydrobiology, 17:41-47.

Delbecque, E.J.P. and Chatrou, A.H.C., 1983. A comparison of the periphyton of *Nuphar lutea* and *Nymphaea alba*. The distribution of multicellular algae and *Vorticella* spp. on the undersides of floating leaves. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18-23 September, 1983: pp.57-62.

Delbecque, E.J.P., 1985. Periphyton on nymphaeids: An evaluation of methods and separation techniques. Hydrobiologia, 124:85-93.

Den Hartog, C., 1976. Aquatische Oecologie en Waterplanten. Inaugurale rede, Katholieke Universiteit, Nijmegen, 18 pp.

Den Hartog, C., 1978. Structural and functional aspects of macrophyte-dominated aquatic systems. Proc. E.W.R.S. 5th. Symp. on Aquatic Weeds (Amsterdam), pp.35-41.

Den Hartog, C., 1983. A short survey of the research topics of the Laboratory of Aquatic Ecology, Catholic University, Nijmegen, including a literature list. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18-23 September, 1983, pp.1-15.

Giesen, Th.G. and Van der Velde, G., 1978. De verspreiding van *Nymphaea candida* Presl en *Nymphaea alba* L. in Nederland. Gorteria, 9:61-66.

Giesen, Th.G. and Van der Velde, G., 1983. Ultraviolet reflectance and absorption patterns in flowers of *Nymphaea alba* L., *Nymphaea candida* Presl and *Nuphar lutea* (L.)Sm. (Nymphaeaceae). Aquat. Bot., 16:369-376.

Heijs, F.M.L., 1984. Annual biomass and production of epiphytes in three monospecific seagrass communities of *Thalassia hemprichii* (Ehrenb.)Aschers. Aquat. Bot., 20:195-217.

Jacobs, R.P.W.M., 1982. Component studies in seagrass ecosystems along West European coasts. Thesis Catholic University, Nijmegen, 216 pp.

Lammens, E.H.R.R. and Van der Velde, G., 1978. Observations on the decomposition of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae) with special regard to the leaves. Aquat. Bot., 4:331-346.

Roelofs, J.G.M., 1983. Impact of acidification and eutrophication on macrophyte communities in soft waters in The Netherlands. I. Field observations. Aquat. Bot., 17:139-155.

Roelofs, J.G.M., Schuurkes, J.A.A.R. and Smits, A.J.M., 1984. Impact of acidification and eutrophication on macrophyte communities in soft waters. II. Experimental studies. Aquat. Bot., 18:389-411.

Roijackers, R.M.M., 1983. Primary productivity of the phytoplankton in the Oude Waal near Nijmegen. A comparison between the nymphaeid dominated zone and the open water zone. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18-23 September, 1983: pp.203-207.

Roijackers, R.M.M., 1984. Some structural characteristics of the phytoplankton in the Oude Waal near Nijmegen, The Netherlands. Verh. Internat. Verein. Limnol., 22:1687-1694.

Van der Velde, G., 1978. Structure and function of a nymphaeid dominated system. Proc. E.W.R.S 5th Symp. on Aquatic Weeds (Amsterdam), pp.127-133.

Van der Velde, G., 1980. Studies in nymphaeid-dominated systems, with special emphasis on those dominated by *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae). Thesis Catholic University, Nijmegen, 163 pp.

Van der Velde, G. and Brock, Th.C.M., 1980. The life history and habits of *Notiphila brunnipes* R.-D. (Diptera, Ephydridae), an autecological study on a fly associated with nymphaeid vegetation. Tijdschr. Ent., 123:105-127.

Van der Velde, G. and Peelen-Bexkens, P.M.M., 1983. Production and biomass of floating leaves of three species of Nymphaeaceae in two Dutch waters. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18-23 September, 1983, pp.230-235.

Van der Velde, G. and Van der Heijden, L.A., 1981. The floral biology and seed production of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae). Aquat. Bot., 10:261-293.

Van der Velde, G. and Van der Heijden, L.A., 1985. Initial decomposition of floating leaves of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae) in relation to their age, with special attention to the role of herbivores. Verh. Internat. Verein. Limnol., 22:2937-2941.

Van der Velde, G., Brock, Th.C.M., Heine, M. and Peeters, P.M.P.M., 1978. Flowers of Dutch Nymphaeaceae as a habitat for insects. Acta Bot. Neerl., 27:429-430.

Van der Velde, G., Van der Heijden, L.A., Van Grunsven, P.A.J. and Bexkens, P.M.M., 1982. Initial decomposition of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae), as studied by the leaf-marking method. Hydrobiol. Bull. (Amsterdam), 16:51-60.

Van Vierssen, W., 1982. The ecology of communities dominated by *Zannichellia* taxa in Western Europe. Thesis Catholic University, Nijmegen, 224 pp.

Van Wijk, R.J., 1983. Life-cycles and reproductive strategies of *Potamogeton pectinatus* L. in The Netherlands and the Camargue (France). Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18-23 September, 1983: pp.317-321.

Verhoeven, J.T.A., 1980. The ecology of *Ruppia*-dominated communities in Western Europe. Thesis Catholic University, Nijmegen, 222 pp.

REMARKS ON THE DISTRIBUTION AND SURVIVAL BIOLOGY OF THE WHITE, YELLOW AND FRINGED WATERLILY
AN INTRODUCTION.

Nuphar lutea (L.)Sm. and Nymphaea alba L. (Nymphaeaceae).

Distribution and ecological amplitude.

In Europe, the geographical ranges of *Nuphar lutea* (Yellow waterlily) and *Nymphaea alba* (White waterlily) (Figure 1) largely overlap. Both species occur throughout Europe, from Scandinavia to the Mediterranean and from Ireland far into Russia (Meusel et al., 1965). The distribution patterns of these species depend on the presence of suitable habitats for growth and survival in their established phase, as well as on the effectiveness of dispersal in the past to suitable habitats where the seeds could germinate and the seedlings could develop into full-grown plants. In many localities, however, these nymphaeid species have been introduced by man as full-grown plants because of their ornamental qualities.

In their ranges of tolerance for chemical and physical habitat factors *Nuphar lutea* and *Nymphaea alba* show a large overlap, at least in their established phase. They can be regarded as indifferent to several chemical parameters, such as the alkalinity and the nitrogen and phosphorus content of the water (Wiegleb, 1978, Roelofs, 1985), and they tolerate a fair degree of eutrophication and acidification. According to Aulio (1980), *Nuphar lutea* is not harmed by high levels of copper in the sediment. Pollutants such as detergents, however, may affect the vitality of *Nuphar* and *Nymphaea* (Agami et al., 1976). Both species occur on several types of fine-textured substrates, such as clay, sand and peat (Luther, 1951; Heslop-Harrison, 1955 a and b; Haslam, 1977), and tolerate a high organic matter content and strongly reduced conditions in the bottom. In the Netherlands both *Nuphar lutea* and *Nymphaea alba* can be found in waters varying from acidified moorland pools (e.g. the Voorste Choorven near Oisterwijk) to alkaline eutrophic lakes (e.g. the Oude Waal). *Nuphar lutea*, however, has its optimum towards alkaline, nutrient-rich habitats, while *Nymphaea alba* occurs more often in softer waters with a lower nutrient status (see also Heslop-Harrison, 1955a and b).

Figure 1: *Nuphar lutea* (above) and *Nymphaea alba* (below).

Both *Nuphar lutea* and *Nymphaea alba* grow in stagnant and slow-moving water, generally not exceeding a depth of ca. 3 m. In large, shallow aquatic ecosystems, severe winds and water movements restrict them to more or less sheltered localities. Furthermore, in lakes and canals they may be restricted to the edges as a result of physical damage caused by boats. In the growing season *Nuphar lutea* and *Nymphaea alba* tolerate extremely high water levels, such as occasionally occur e.g. in backwaters of the river Waal for relatively short periods; as long as the bottom remains moist they can also survive emergence in summer (Van der Velde, 1980, Brock et al., accepted). Although both species show a considerable overlap in their tolerance for several physical habitat factors, some conspicuous differences also exist. *Nuphar lutea* tolerates more wave action than *Nymphaea alba* and consequently can be found more often in the relatively exposed parts of a lake, while *Nymphaea alba* can more frequently be found in the shelter of emergent macrophytes (Ross, 1937; Luther, 1951). Furthermore, *Nuphar lutea* is more common in slow-moving waters and occurs more often along river banks (Heslop-Harrison, 1955a and b).

Notes on the biology of the established plants.

When fully grown, both *Nuphar lutea* and *Nymphaea alba* possess stout, irregularly branched rhizomes. The rhizome of *Nuphar* usually creeps over the bottom, while the older parts of the *Nymphaea* rhizome are more often found in the sediment. The rhizomes of both species are firmly anchored in the sediment by roots, which in the case of *Nuphar* may reach a length of ca. 75 cm, while some of the roots of *Nymphaea* may penetrate the substrate to a depth exceeding 1 m. The root stocks of both species generally have a very slow turnover. Precise data on the possible life-span of root stocks in nature are not available. The root stocks grow at their apices, while the oldest parts slowly decompose. According to Heslop-Harrison (1955a and b) the size of individual *Nuphar* and *Nymphaea* plants in nature suggests persistence for several decades. Katanskaya (1960; in Luther, 1983) reported that in a 42 m^2 area in lake Saari-Jarvi (Finland), two rhizomes of *Nuphar lutea* had a total length of ca. 28.5 m if the lengths of the two main branches and several lateral branches were added up. Glück (1924) gives a drawing of a rhizome of *Nuphar lutea* with a total length exceeding 6 m. In the Oude Waal rhizomes of *Nuphar* and

Nymphaea with a total length of several metres have been observed. Here, the underground plant parts (roots and root stocks) of *Nuphar* and *Nymphaea* take shares of 52 % and 75 % respectively, of the total peak biomass (Figure 2). In lake Vitalampa (Sweden) the underground structures of *Nuphar* accounted for more than 80 % of the total peak biomass (Erikson, 1973).

Due to many years of biomass accumulation the underground parts of *Nuphar* and *Nymphaea* may contain large amounts of stored resources which can be used for the growth of the aboveground structures in spring or after severe damage of the leaves during the growing season. The seasonal changes in the specific weight of the root stocks of *Nuphar* and *Nymphaea*, as observed by Stemkens and Meekes (1978) in the Oude Waal, suggest a net translocation of stored substances to the aboveground parts in spring and early summer, and the reverse at the end of the growing season (Figure 3). The differences in specific weight of the *Nuphar* and *Nymphaea* rhizomes in autumn and spring suggest that the root stocks use a portion of the stored resources for respiration during the winter.

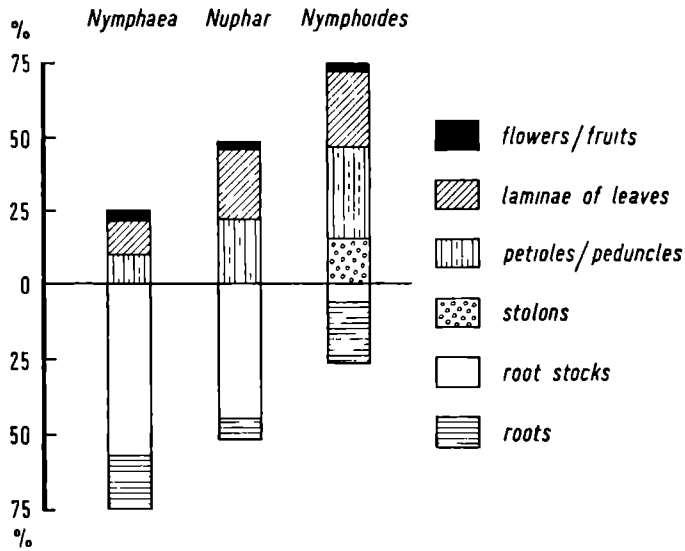

Figure 2: The relative biomass contributions (ash-free dry weight) of the different plant parts of *Nymphaea alba*, *Nuphar lutea* and *Nymphoides peltata* in the Oude Waal at the time of their peak biomass.

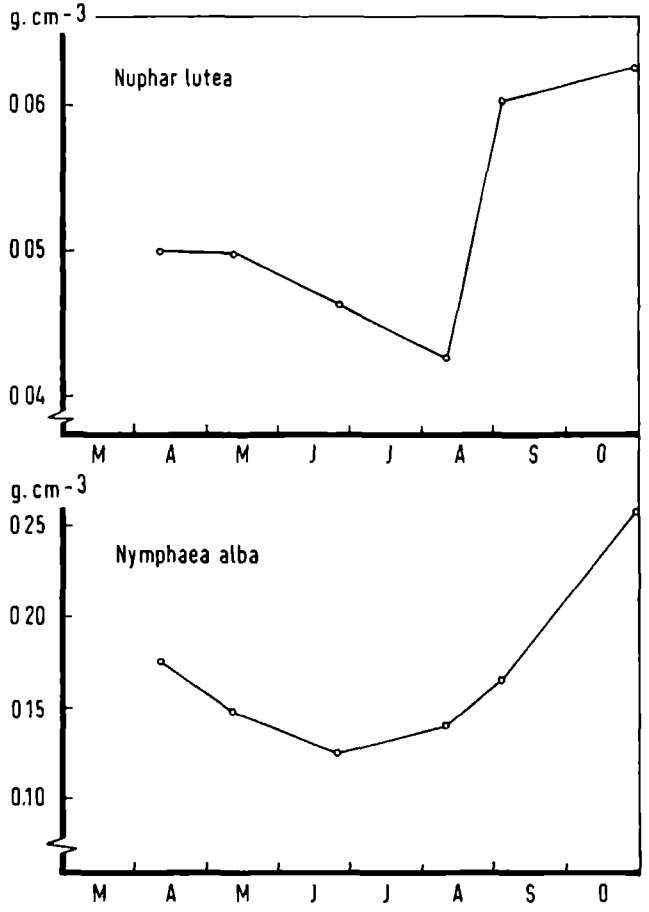

Figure 3: The seasonal changes in the specific weight (g ash-free dry weight/m^3) of the apices of root stocks of *Nuphar lutea* and *Nymphaea alba* in the Oude Waal in 1978.

When fully grown, nymphaeids may possess leaves of three kinds; those which are located some cms above the surface of the water (aerial leaves), those which float at the surface of the water (floating leaves) and those which are permanently submerged (submerged leaves). Under comparable environmental circumstances (e.g. the same water depth), aerial leaves are more common in *Nymphaea alba* and submerged leaves in *Nuphar lutea*. The capability of *Nymphaea alba* to produce a large number of leaves per m^2 (crowding) and to elevate part of its leaves above the water is one of the reasons why this species usually has a higher aboveground peak biomass per m^2 in the Oude Waal than

Nuphar lutea (Figure 4). Furthermore, this capability might also explain why *Nymphaea alba* is more successfully competing for space with e g. littoral emergent macrophytes (see also Luther, 1951).

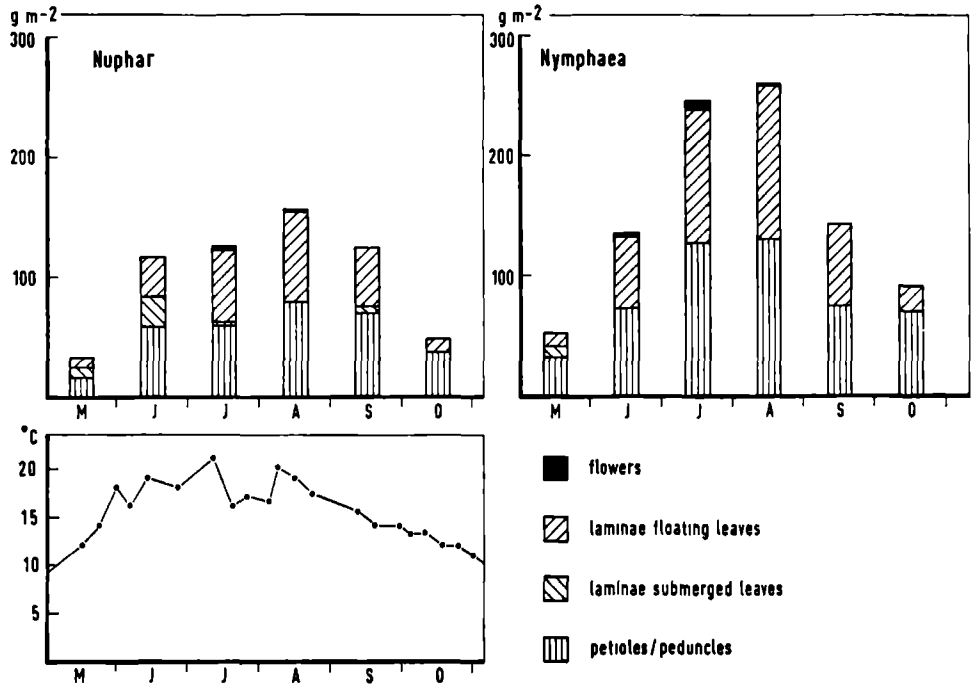

Figure 4: The changes in the mean monthly aboveground biomass (A.F.D.W.) of *Nuphar lutea* and *Nymphaea alba* in 1 m^2 plots, and the changes in water temperature in the Oude Waal in 1977 (changed after Van der Velde and Peelen-Bexkens, 1983).

The laminae of the floating and aerial leaves have hydrophobic upper surfaces and may reach a length of up to 30-35 cms in the Oude Waal. Although the laminae of both species are rather pliable, those of *Nymphaea* are considerably more rigid than those of *Nuphar*. This phenomenon might explain, at least in part, why *Nymphaea alba* is less tolerant for the action of the waves.

The laminae of the submerged leaves of *Nuphar lutea*, with a length and width of up to ca. 30 cm, are relatively thin and very pliable. Submerged leaves of *Nuphar* can be present throughout the year. Particularly at the end of the winter and in spring, before the development of a dense floating leaf

canopy, the biomass of the submerged leaves may be relatively high in *Nuphar* (see Figure 4). At the time of its peak biomass, when the floating leaves are also at a maximum, *Nuphar lutea* possesses few or no submerged leaves. This phenomenon can largely be explained by the shading of the water column. In flowing waters and, depending on the clarity of the water, at deeper sites (>3 m) in stagnant habitats, *Nuphar lutea* plants may occur with submerged leaves only. According to Twilley et al.(1977) the heterophyllous habit of *Nuphar* allows it to assume the role of a submerged macrophyte in winter, when submerged leaves persist, but not floating leaves. During summer, when leaves of both types are present, the floating leaves appear to specialize in photosynthesis, while the submerged leaves may be of importance at that time for the uptake of nutrients from the water. The thin submerged leaves are better adapted for nutrient absorption than the thick, leathery floating leaves (Twilley et al., 1977). In the established phase *Nymphaea alba* may also possess some submerged leaves, but these are usually smaller than those of *Nuphar* and can normally be found only in winter and early spring (see e.g. Figure 4).

Generally speaking, *Nuphar lutea* and *Nymphaea alba* show a comparable phenology in The Netherlands. The floating leaves of both species can be observed from May to November and they mostly reach their aboveground peak biomass in August (Figure 4). In the Oude Waal the total number of floating (and aerial) leaves produced per m^2 per year is higher for *Nymphaea alba* than for *Nuphar lutea*, while the mean leaf persistence is also somewhat higher in the case of *Nymphaea* (Table 1). The number of leaves produced and the leaf persistence clearly depend on factors such as geographical latitude and the trophic status of the locality, the presence of certain herbivores and pathogens and the action of wind and waves. Observations in the field suggest that in The Netherlands the mean leaf persistence of *Nuphar* and *Nymphaea* is higher under more nutrient-poor conditions.

In The Netherlands, flowers of *Nuphar* and *Nymphaea* are usually found in June, July and August. In the Oude Waal ca. 7-10 *Nuphar* flowers and ca. 8-21 *Nymphaea* flowers may be produced per m^2 per year in stands dominated by these nymphaeids. The flowers of both species are visited by various insects which may cause cross-pollination (see e.g. Van der Velde and Brock, 1980).

Notes on the biology of seeds and seedlings

On an average the fruits of *Nuphar lutea* in the Oude Waal contain 195 seeds and those of *Nymphaea alba* 872 (Van der Velde et al., 1978) The seeds can be transported to suitable habitats by the river water during periods of flooding, or by water birds and sometimes by fish (Heslop-Harrison, 1955a and b; Ross, 1937). According to Guppy (1897), most seeds of *Nuphar* and *Nymphaea* do not germinate in the year of production and, under the proper conditions, remain viable for several years; the seeds of both species are killed by long periods of desiccation. Although the seeds of both species germinate fairly easily in the laboratory (see e.g. Heslop-Harrison, 1955a and b), the conditions necessary for a successful establishment of seedlings are rather rare in nature, since they are not often found in aquatic ecosystems where full-grown plants of *Nuphar* and *Nymphaea* occur. In the Oude Waal seedlings of *Nymphaea alba* and *Nuphar lutea* have been observed only in 1976, a year with extremely low water levels and high water temperatures due to very dry climatological circumstances. The seedlings were found in shallow clear pools within the desiccated area of this system. However, when the overlying water of these pools evaporated the seedlings died. In years with higher water levels, growth of seedlings of *Nuphar* and *Nymphaea* is inhibited in the Oude Waal; under such conditions the seedlings are shaded by the turbid water and/or by the floating leaves of the full-grown nymphaeids. In the first years, seedlings of *Nuphar* and *Nymphaea* possess submerged leaves only and cannot survive emergence (Brock et al., accepted). A normal development of seedlings to full-grown plants can in all likelyhood take place only in more or less permanent habitats with clear water.

Since both species in their established phase tolerate a fair degree of eutrophication, acidification and pollution, and since *Nuphar lutea* has its optimum in alkaline, nutrient-rich habitats and *Nymphaea alba* in softer waters with a lower nutrient status, it seems likely that there are differences between these species in the effectiveness of seed dispersal and/or in the tolerance ranges of the seedlings for certain habitat factors.

Distribution and ecological amplitude.

Nymphoides peltata (Fringed waterlily) (Figure 5) occurs in central, western and southern Europe, northern and western Asia, Kashmir, the Himalayas and Japan, and it has also been introduced in North America (Glück, 1924; Stuckey, 1974). In Europe the northern limit of its distribution coincides more or less with the 16°C July isotherm (Van der Velde et al., 1979). Compared to *Nuphar lutea* and *Nymphaea alba*, *Nymphoides peltata* does not occur as far north in Europe. For a detailed map of its geographical distribution the reader is referred to Meusel et al.(1978).

Nymphoides peltata has its optimum in eutrophic alkaline systems (Grote, 1980; Casper and Krausch, 1981) on mineral soils, particularly clay (Döhler, 1963; Westhoff et al., 1971; Bloemendaal and Schuurkes, 1981). Although this species also occurs on mineral soils with a relatively high organic matter content (Grote, 1980; Bloemendaal and Schuurkes, 1981) it probably does not tolerate too great an accumulation of organic material (Van der Voo and Westhoff, 1961; Westhoff et al., 1971). *Nymphoides* is more or less indifferent to eutrophication, but, according to Bloemendaal and Schuurkes (1981), it does not tolerate high ammonia and/or detergent levels. It grows in stagnant and slow moving waters, generally not deeper than ca. 3 m. According to Funke (1951) *Nymphoides peltata* shows an optimum growth at a water depth of 20-150 cm. Although this species is able to colonize large areas in suitable shallow aquatic ecosystems, severe wave action may restrict it to the edges.

In The Netherlands, *Nymphoides peltata* is very common in backwaters of the large rivers, particularly those which are regularly flooded by river water in winter (Van der Voo and Westhoff, 1961). However, such inundations during the growing season, which result in a sudden rise of the water level of several metres, diminish its vitality or even cause its disappearance. On the other hand *Nymphoides peltata* tolerates extremely low water levels and emergence in the growing season very well (Brock et al., accepted).

Table I.
The number of floating and (aerial) leaves produced per m^2 per year (= N) and the mean leaf persistence in days (= P) of the nymphaeids studied.

Species Locality	N	P	Source
Nuphar lutea			
Oude Waal 1976	122	39.2	2, 4
Oude Waal 1977	59	38.4	2, 4
Haarsteegse Wiel 1977	77	49.9	2, 4
Lake Vitalampa (Sweden)	-	60-80	1
Nymphaea alba			
Oude Waal 1976	180-195	39.3	2, 4
Oude Waal 1977	108	46.2	2, 4
Nymphoides peltata			
Oude Waal 1976	-	18.2	2
Bemmelse Strang 1980	1108-1712	23.1-30.1	3, 5

(1) Erikson, 1973; (2) Van der Velde, 1980; (3) Van der Velde et al.,1982
(4) Van der Velde and Peelen-Bexkens, 1983; (5) Van der Velde et al.,subm.

Figure 5: A stand of *Nymphoides peltata*.

Notes on the biology of the established plants

In the established phase, *Nymphoides peltata* possesses several relatively small root stocks, which are interconnected by stolons (see Figure 2 in chapter 3). The root stocks (short shoots) are ca. 0.5-15 cm in length, have a diameter of ca. 0.48-0.70 cm, are whitish in colour and are anchored in the bottom by means of roots. These roots may penetrate into the bottom to a depth of ca. 40 cm. The stolons (long shoots) are green, creep over the bottom and have a length of ca. 16.5-122 cm (Van der Velde et al., 1979) Through vegetative propagation by stolons, *Nymphoides peltata* has the potential to colonize large areas within a few years, at least as long as no competition with other nymphaeids occurs. In comparison with *Nuphar lutea* and *Nymphaea alba*, *Nymphoides peltata* has a relatively small proportion of its peak biomass below ground (Figure 2). Furthermore, the turnover of the underground plant parts of *Nymphoides* is high in comparison with that of the rhizomes of *Nuphar* and *Nymphaea*. In the Bemmelse Strang, the mean persistence of the underground plant parts of *Nymphoides* has been estimated as ca. 18 months (see chapter 3). This life span is long enough for the roots and root stocks to function as hibernating organs.

In The Netherlands the floating leaves of *Nymphoides peltata* can usually be found in the period from May to November. The length of the more or less roundly cordate leaf-blades (up to 15 cm) varies with the type of habitat, the time of the year in which they are produced and whether they originate from the root stocks or stolons near the bottom or from the flowering stems near the surface of the water (Van der Velde et al., 1979). Both the leaf-blades and their petioles are very pliable, which may explain the tolerance *Nymphoides* shows for a fair amount of buffeting of the waves, at least under normal water level regimes.

In aquatic systems where *Nymphoides peltata* occurs together with one of the Nymphaeaceae, it is largely restricted to a belt between the littoral emergent macrophytes and the vegetation dominated by *Nuphar* and/or *Nymphaea* at the deeper sites, due to a vigorous competition for space among these nymphaeids. In relatively young backwaters, in which *Nuphar* and/or *Nymphaea* have not yet settled, *Nymphoides peltata* may colonize large areas, including the relatively deep sites.

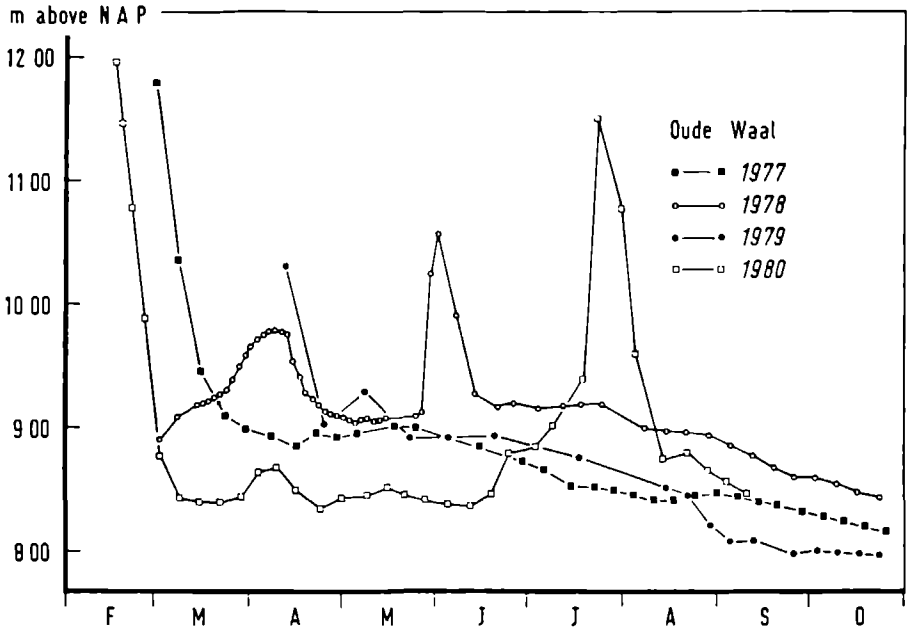

Figure 6: Water level fluctuations in the course of several years in the Oude Waal. In 1980 there was a sudden rise in water level due to an inundation by the river Waal during the growing season (N.A.P. = mean Dutch sea level) (after Brock, Van der Velde and Van de Steeg, accepted).

As was the case with the underground plant parts, the leaves of *Nymphoides* have a much higher turnover and a shorter persistence than those of *Nuphar* and *Nymphaea* (Table I). The total number of leaves produced per m^2 is also much higher for *Nymphoides* than for the other nymphaeids. Furthermore, newly-formed floating leaves of *Nymphoides* reach the surface of the water within a remarkably short time. Funke (1951) observed that the petioles of the young leaves can grow ca. 1 cm/h during the first days by means of cell elongation. This vigorous growth, however, may be a disadvantage under certain circumstances. In the summer of 1980, after a rise in the water level in the Oude Waal of ca. 3 metres due to inundation by the river Waal (Figure 6), it was observed that the floating leaves of *Nymphoides*, *Nuphar* and *Nymphaea* had disappeared under water. In these circumstances, only the petioles of the younger leaves still had the capacity to elongate in order to allow the leaf-blades to reach the surface of the water, while the older leaves ultimately decomposed. The leaves of *Nymphoides* were the first to reach the water surface again during the period of high

water levels. The leaf stalks, however, had become very fragile. As a consequence, all new leaves of *Nymphoides* washed away as a result of wind and wave action. The leaves of *Nuphar* and *Nymphaea* reached the surface of the water several days later, when the water level had already dropped considerably. Furthermore, the thicker petioles of *Nuphar* and *Nymphaea* remained firm and were less fragile after elongation. In 1981, the year after the summer inundation, *Nymphoides peltata* had disappeared completely from the Oude Waal, while *Nuphar* and *Nymphaea* had survived. After a complete inundation during the growing season, nymphaeids have to reallocate organic matter from the underground parts, in order to allow the production of new floating leaves. Although *Nymphoides* appeared to be very successful in reaching the surface of the water again, this probably also resulted in the exhaustion of most of its stored resources. The washing away of newly formed leaves after the inundation was, therefore, ultimately disastrous for *Nymphoides peltata*. Furthermore, oxygen depletion and the formation of toxic respiration products in the underground parts, due to anaerobic respiration, may also have played a part in the disappearance of *Nymphoides* (Brock et al., accepted).

For more information concerning the growth and annual biomass production by *Nymphoides peltata* in its established phase the reader is referred to the second chapter of this thesis.

Notes on the biology of seeds and seedlings.

Not only in its established phase but also in its reproductive phase, *Nymphoides peltata* can be considered a typical pioneer, in that it is able to produce a very large number of seeds. According to Van der Velde and Van der Heijden (1981) the mean number of flowers produced per m^2 of a *Nymphoides*-stand in the Oude Waal was 180 in 1979 (a year with a normal water level regime). These flowers are visited by insects, which may result in cross-pollination. The average number of seeds developed per fruit was 26.5, so that the mean number of seeds produced per m^2 was 3117 in 1979 (Van der Velde and Van der Heijden, 1981). In years in which aquatic ecosystems in the river forelands are flooded by river water in summer, the seed production is usually much smaller.

For the first days after their release from the fruits the seeds float at the water surface, later on they sink to the bottom. The seeds can be dispersed by wind over the water, by river water during periods of flooding, or by water birds.

According to Guppy (1897), most seeds of *Nymphoides peltata* do not germinate in the year of production, and under the proper conditions they remain viable for several years; *Nymphoides* seeds still germinate after several months of desiccation while the seeds of *Nuphar* and *Nymphaea* are killed under these circumstances (Guppy, 1897). In the Oude Waal the seeds of *Nymphoides peltata* have been found to germinate on wet mud with hardly any overlying water. The seedlings also survived under such circumstances. In 1976, when the Oude Waal dried up almost completely, numerous seedlings of *Nymphoides peltata* were observed over the entire area of this oxbow lake (even in the *Nuphar* and *Nymphaea* stands). These seedlings developed into full-grown plants within one growing season. In normal years seedlings of *Nymphoides* were only found on very shallow sites near the littoral helophyte zone and never in deeper turbid water or below the dense floating leaf canopies of the nymphaeids (Brock et al., accepted).

Concluding remarks.

Nymphoides peltata has a well-developed capacity to establish itself within a short time in suitable habitats, particularly on clay bottoms in shallow backwaters of fluviatile areas and in ditches and canals of polders. In these areas it is usually the first nymphaeid to appear in new aquatic habitats, such as recently excavated clay pits. *Nymphoides peltata* can be regarded as a typical pioneer because of its high seed production, the massive germination of its seeds on emerged bottoms, the rapid development of its seedlings into full-grown plants and its capacity to colonize large areas within a few years by means of vegetative propagation. The common occurrence of this species in backwaters of the large rivers which are regularly flooded by river water in winter and early spring (Van der Voo and Westhoff, 1961) may be explained by the efficient seed dispersal by river water and by the maintenance of suitable bottom conditions due to the washing away of organic matter and the sedimentation of clay during and after the floodings. The disappearance of *Nymphoides peltata* from backwaters of the large rivers after extremely high water levels during the growing season may be explained by the relatively rapid exhaustion of the stored resources. Using the classification of Grime (1979),

Nymphoides peltata can be regarded as a species with "ruderal" characteristics.

The establishment of *Nuphar lutea* and *Nymphaea alba* in suitable habitats is a relatively slow process. The growth of the seedlings into plants with floating leaves and a well-developed root stock takes several years. In comparison with *Nymphoides peltata* they invest more energy in the building up of a large biomass resource below ground and less in a rapid colonization of the area by means of vegetative propagation. Using the classification of Grime (1979) *Nuphar lutea* and *Nymphaea alba* can be regarded as plants with "competitor" characteristics. When *Nuphar lutea* and *Nymphaea alba* have established themselves they can live as individual plants for several decades. They can withstand eutrophication, acidification and accumulation of organic material in the bottom, as well as disturbances such as exceptional high water levels during the growing season. Such disturbances are tolerated because of the large biomass resources below ground. At least two reasons can be mentioned why the full-grown plants are more or less indifferent to the trophic status of the system:

1) In waters enriched with nitrogen and phosphorus the photosynthesis of the floating leaves is not affected by the shading effect of phytoplankton blooms and/or a dense growth of epiphytes.
2) In acidified waters the photosynthesis of the floating leaves is not limited by a shortage of inorganic carbon in the water because carbon dioxide can enter these plants through the stomata at the upper surface of the floating leaves.

The capacity of the established plants to grow in sediments rich in organic matter may depend to a large extent on oxygen transport from the floating leaves to the roots, since oxygen is needed for the respiration of the underground parts and, according to Armstrong (1978), oxygen contributes to the detoxification of the rhizosphere in strongly reduced sediments. *Nuphar lutea* and *Nymphaea alba* have a well-developed aerenchyma which enables the transport of atmospheric oxygen to the underground plant parts. Furthermore, Dacey (1981) and Dacey and Klug (1982) demonstrated that several *Nuphar* species have a flow-through ventilation system. In these *Nuphar* species an elevated pressure in the young leaves drives a bulk flow of gas down the petioles of the young leaves to the rhizome, and from

the rhizome via the petioles of the older leaves back to the atmosphere again. According to Dacey (1981) and Dacey and Klug (1982) raised temperatures at the young leaf-blades play a fundamental role in this pressurization. It is quite possible that *Nuphar lutea* and *Nymphaea alba* also have such a flow-through ventilation system. It is evident that such a ventilation system is highly advantageous to nymphaeids growing in strongly reduced sediments.

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References

Agami, M., Litav, M. and Waisel, Y., 1976. The effects of various components of water pollution on the behaviour of some aquatic macrophytes of the coastal rivers of Israel. Aquat. Bot., 2:203-213.

Armstrong, W., 1978. Root aeration in wetland conditions. In: Hook, D.D. and Crawford, R.M.M. (eds.), Plant life in anaerobic environments. Ann Arbor Science Publishers, Ann Arbor, M.I., pp.269-297.

Aulio, K., 1980. Accumulation of copper in fluvial sediments and yellow water lilies (*Nuphar lutea*) at varying distances from a metal processing plant. Bull. Environm. Contam. Toxicol., 25:713-717.

Bloemendaal, F. and Schuurkes, R., 1981. Een onderzoek naar de verspreiding van waterplanten in relatie tot het abiotisch milieu, met name in matige en hoog-alkaliene wateren. Report no. 136 of the Laboratory of Aquatic Ecology, Catholic University Nijmegen, 60 pp.

Brock, Th.C.M., Van der Velde, G. and Van der Steeg, H.M., accepted. The effects of extreme water level fluctuations on the wetland vegetation of a nymphaeid-dominated oxbow lake in The Netherlands. Arch. Hydrobiol. Suppl. (accepted).

Casper,S.J. and Krausch, H.-D., 1981. Süsswasserflora von Mitteleuropa. Begründet von A. Pascher. Band 24: Pteridophyta und Anthophyta, 2. Teil: Saururaceae bis Asteraceae. Gustav Fischer Verlag, Stuttgart, New York, 942 pp.

Dacey, J.W.H., 1981. Pressurized ventilation in the yellow waterlily. Ecology, 62:1137-1147.

Dacey, J.W.H. and Klug, M.J., 1982. Ventilation by floating leaves in *Nuphar*. Am. J. Bot., 69:999-1003.

Döhler, H., 1963. Die Seekanne, unser einziges wasserbewohnendes Enziangewächs. Kosmos, 59:254-257.

Erikson, F., 1973. Makrofyterna och deras produktion i sjön Vitalampa (Klotenprojectet Rapport no. 2). Scr. Limnol. Upsal., 346:1-36.

Funke, G.L., 1951. Waterplanten. J. Noorduijn en zoon N.V., Gorinchem, 250 pp.

Glück, H., 1924. Biologische und morphologische Untersuchungen über Wasser- und Sumpf-gewächse IV. Untergetauchte und Schwimmblattflora. Gustav Fischer, Jena, 746 pp.

Grime, J.P., 1981. Plant strategies and vegetation processes. John Wiley & Sons. Chichester, New York, Brisbane, Toronto, 222 pp.

Grote, E., 1980. Zur Verbreitung der Seekanne im Gebiet von Ems und Hase mit Bemerkungen zu den Biotopansprüchen. Inf. Natursch. Landschaftpfl., 2 142-153.

Guppy, H.B., 1897. On the postponement of the germination of the seeds of aquatic plants. Proc. Roy. Phys. Soc., Edinburgh, 13:344-359.

Haslam, S.M., 1971. Physical factors and some river weeds. Proc. Eur. Weed Res. Coun. 3rd Int. Symp. Aquatic Weeds, 1971, pp.29-39.

Heslop-Harrison, Y., 1955a. *Nuphar* Sm.. Biological flora of the British Isles. J. Ecol., 43 342-364.

Heslop-Harrison, Y., 1955b. *Nymphaea* L. em. Sm. (nom. conserv.). Biological flora of the British Isles. J. Ecol., 43:719-734.

Luther, H., 1951. Verbreitung und Ökologie der hoheren Wasserpflanzen im Brackwasser der Ekenas-gegend in Südfinnland. Acta Bot. Fennica, 50:1-370.

Luther, H., 1983. On life-forms, and aboveground and underground biomass of aquatic macrophytes. Acta Bot. Fennica, 123:1-23.

Meusel, H., Jäger, E. and Weinert, E., 1965. Vergleichende Chorologie der zentraleuropäischen Flora. Vol.1: Text 583 pp., Vol.2: Karten, 1-258. Gustav Fischer Verlag, Jena.

Meusel, H., Jäger, E., Rauschert, S. and Weinert, E., 1978. Vergleichende Chorologie der zentraleuropäischen Flora. Band III. Text, 418 pp.: Karten, 259-421. Gustav Fischer Verlag, Jena.

Roelofs, J.G.M., 1985. Waterkwaliteit en waterplanten, 15 pp. In: Programma pao-cursus, "Waterkwaliteit landelijk gebied; aspekten van kwaliteitsbeheer", L.H. Wageningen, Stichting Post-Academisch Onderwijs.

Ross, H., 1937. Familie Nymphaeaceae. Chapter 41. In: Von Kirchner, O., Loew, E. and Schröter C., (eds.), Lebensgeschichte der Blütenpflanzen mitteleuropas. Lief. 55/56. Bd.2, Abt. 3, Bogen 1-6. Verlagsbuchhandlung Eugen Ulmer, Stuttgart, pp.1-50.

Stemkens, T., and Meekes, H., 1978. Een onderzoek naar de rol van de bodem en de macrofyten in de nutriënten-cyclus en naar de biomassa van de macrofyten in de Oude Waal bij Nijmegen en de Haarsteegse Wiel bij Vlijmen. Rapport no. 100, Laboratorium voor Aquatische Oecologie, Katholieke Universiteit Nijmegen, 61 pp.

Stuckey, R.L., 1974. The introduction and distribution of *Nymphoides peltatum* (Menyanthaceae) in North America. Bartonia, 42:14-23.

Twilley, R.R., Brinson, M.M. and Davis, G.J., 1977. Phosphorus absorption, translocation and secretion in *Nuphar lutea*. Limnol. Oceanogr., 22:1022-1031.

Van der Velde, G., 1980. Studies in nymphaeid-dominated systems, with special emphasis on those dominated by *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae). Thesis Catholic University, Nijmegen, 163 pp.

Van der Velde, G. and Brock, Th.C.M., 1980. The life history and habits of *Notiphila brunnipes* R.-D. (Diptera, Ephydridae), an autecological study on a fly associated with nymphaeid vegetation. Tijdschr. Ent., 123:105-127.

Van der Velde, G. and Peelen-Bexkens, P.M.M., 1983. Production and biomass of floating leaves of three species of Nymphaeaceae in two Dutch waters. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18-23 September, 1983, pp.230-235.

Van der Velde, G. and Van der Heijden, L.A., 1981. The floral biology and seed production of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae). Aquat. Bot., 10:261-293.

Van der Velde, G., Brock, Th.C.M., Heine, M. and Peeters, P.M.P.M., 1978. Flowers of Dutch Nymphaeaceae as a habitat for insects. Acta Bot. Neerl., 27:429-430.

Van der Velde, G., Giesen, Th.G. and Van der Heijden, L., 1979. Structure, biomass and seasonal changes in biomass of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae), a preliminary study. Aquat. Bot., 7:279-300.

Van der Velde, G., Van der Heijden, L.A., Van Grunsven, P.A.J. and Bexkens, P.M.M., 1982. Initial decomposition of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae), as studied by the leaf-marking method. Hydrobiol. Bull. (Amsterdam), 16:51-60.

Van der Velde, G., Van der Heijden, L.A., Van Grunsven, P.A.J. and Bexkens, P.M.M., submitted. Development and productivity of the floating leaves of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae). Aquat. Bot., submitted.

Van der Voo, E.E. and Westhoff, V., 1961. An autecological study of some limnophytes in the area of the large rivers. Wentia, 5:163-258.

Westhoff, V., Bakker, P.A., Van Leeuwen, C.G. and Van der Voo, E.E., 1971. Wilde planten, Flora en vegetatie in onze natuurgebieden. Deel 2, Het lage land. Ver. tot behoud van natuurmonum. in Nederl., 304 pp.

Wiegleb, G., 1978. Untersuchungen über den Zusammenhang zwischen Umweltfactoren und Makrophytenvegetation in stehenden Gewässern. Arch. Hydrobiol., 83:443-484.

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STRUCTURE AND ANNUAL BIOMASS PRODUCTION OF *NYMPHOIDES PELTATA* (GMEL.) O. KUNTZE (MENYANTHACEAE)*

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ABSTRACT

Brock, Th.C.M., Arts, G.H.P., Goossen, I.L.M. and Rutenfr ns, A.H.M., 1983. Structure and annual biomass production of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). *Aquat. Bot.*, 17: 167—188.

In 1980, the monthly changes in biomass and plant surface area, together with aspects of production of *Nymphoides peltata* (Gmel.) O. Kuntze were studied in a backwater of the river Waal (The Netherlands). Furthermore, the seasonal changes in the vertical stratification of the biomass were studied in concrete tanks. These seasonal changes were studied with the harvest method, while the estimation of the net primary production was based upon biomass data and turnover rates of various plant parts. The data thus obtained are compared with those of other water plants, especially other floating-leaved macrophytes. In 1980, *N. peltata* reached its peak biomass in August being 372 g AFDW m^{-2} (ash-free dry weight). The annual net productivity of *Nymphoides* was estimated to be 1036 g AFDW m^{-2}. The leaf blades and their petioles contributed most to the production.

INTRODUCTION

In shallow backwaters of the river Waal (The Netherlands), the floating leaved macrophyte *Nymphoides peltata* (Gmel.) O. Kuntze is common and often represents the dominant vegetation. In 1980 and 1981, the structure and aspects of production, consumption, decomposition and nutrient cycling of *N. peltata* were studied quantitatively in the Bemmelse Strang, an oxbow lake of the river Waal near Nijmegen. In this locality *N. peltata* was found in monospecific stands in a belt with a mean width of 5 m along the western bank. The general scope of the research project and a description of the topographical features of the study site will be given in Van der Velde et al. (1984).

Many shallow fresh waters, such as the Bemmelse Strang, are totally, or at least partly, dominated by macrophytes. During a considerable period of

*Publication No. 23 of the Nymphaeid project.

the year, these water plants form the bulk of the biomass and can be considered as the basic frame of an ecosystem on which most of the other organisms depend in various ways. The way in which a macrophyte fills up the available space, the architecture, is a structural characteristic which can be very decisive for the functioning of the whole system (Den Hartog, 1978, 1982) and is the result of the macrophyte's life strategy under the prevailing environmental conditions. Morphological differentiation differs considerably among aquatic plants; a great number of growth forms based on the habit of the plants can be recognized (Den Hartog and Segal, 1964; Hutchinson, 1975). *Nymphoides peltata* has a nymphaeid growth form, (i.e., a floating-leaved macrophyte which roots in the bottom). Nymphaeids possess leaves that float in essentially a single layer on the water surface and therefore, they effect a vigorous competition for light, particularly because of their capacity to cover the water surface almost completely.

The morphological differentiation of *N. peltata* into roots, short shoots (root stocks), long shoots (stolons), petioles, leaf blades and flowering structures (see Van der Velde et al., 1979) offers a variety of habitats for the accompanying organisms because these organs differ in shape, firmness, spatial orientation and location within the system. An important function of *N. peltata*, which is closely correlated with its structure, is the supply of substrate for periphytic organisms such as algae, bacteria, fungi and various groups of animals. Information on the relative proportions and seasonal fluctuations of the different organs in biomass and substrate supply gives insight, not only in the life strategy of this macrophyte, but also in the role of *N. peltata* for associated organisms.

The biomass and also the primary productivity of *N. peltata* are both important features. The primary production is without doubt the most important function of the macrophyte, because it is decisive for self-maintenance and it results in an energy source affecting various trophic levels of the ecosystem. The *in situ* net primary productivity of large macrophytes with a complex structure, such as nymphaeids, can be estimated in an indirect way by the marking and harvest technique (Waring, 1970; Blanton, 1976). Early studies of aquatic macrophytes often express peak aboveground biomass or seasonal maximum standing crop as annual net production. However, all techniques that measure rates of processes in the field (e.g., growth rates, loss rates, turnover rates) indicate that peak biomass determinations seriously underestimate real production. According to Westlake (1969) peak biomass can only be a useful parameter of production if there are few losses of the current year's production or when these losses can be determined. Furthermore, many years of underground biomass accumulation in certain macrophytes, such as nymphaeids, will tend to overestimate the production of roots and root stocks if seasonal maximum biomass is used. Another basis of many productivity estimates is the finding of Petersen (1913) that annual production of seagrasses is about twice their maximum standing crop. However, as is shown by the results of many in-

vestigator, this formula is not generally applicable for seagrasses (e.g., Jacobs, 1979; Nienhuis and De Bree, 1980) or for freshwater macrophytes (e.g., Westlake, 1982 and literature cited therein). Therefore, in estimating the net primary productivity of *N. peltata* seasonal maximum standing crop data cannot be used without a correction factor.

The net primary productivity of *N. peltata* in the natural locality of the Bemmelse Strang can be estimated by studying the increase in biomass plus the losses due to grazing or decomposition of plant parts. Floating leaves of *N. peltata* continually develop and die off throughout the growing season. Lammens and Van der Velde (1978) and Van der Velde et al. (1982) showed that the decomposition of *N. peltata* leaves can be caused by both internal physiological factors and external factors, such as damage caused by wind and wave action, consumption, damage of the living tissue by animals and infection by microorganisms. These decomposition processes determine the mean leaf persistence and consequently the number of leaf turnovers per growing season. According to Waring (1970) and Blanton (1976) the annual net production for the leaf blades and petioles of *Nuphar advena* Ait. can be calculated by multiplying their average standing crop for the growing season by the number of turnovers.

The objectives of the present paper are:

(1) to describe the seasonal changes in biomass and structure of *N. peltata* in the Bemmelse Strang; and
(2) to give an estimation of the annual net productivity of *Nymphoides.*

MATERIALS AND METHODS

Each month, from February until December 1980, biomass samples of *N. peltata* were harvested from the Bemmelse Strang. The biomass was only harvested in the centre of the *N. peltata* stand on sites with a well-developed vegetation, due to time limitation and to minimize sampling effects on the total vegetation. Due to the sampling procedure applied, the data obtained on architecture, biomass and annual productivity only account for sites where the growth of *N. peltata* was more or less optimal and where there were the least disturbances. At monthly intervals from June until November, when there was a well developed above-ground vegetation, the plants were harvested by hand from 4 quadrats, each with a surface area of 0.25 m^2. In the present study it was decided to harvest and to express the *N. peltata* biomass per unit area of sediment surface. In doing so, the results are not influenced by changes in water level which normally occur in oxbow lakes such as the Bemmelse Strang. Four stakes were used for marking the corners of the quadrat and a straight hoe was used for cutting the edges of the quadrat in the sediment. The above-ground plant parts within the quadrat were gathered first, then all underground parts in each quadrat were removed to a sediment depth of approximately 40 cm. The plant material in each quadrat was placed in polyethylene buckets, washed free

of sediment and detritus, placed in plastic bags and transported to the laboratory.

In winter and early spring it was impossible to harvest *N. peltata* as described above because of the high water levels, low temperatures, high turbidity of the water and a sparse above-ground growth of *N. peltata.* Biomass determinations in this period were made using a cylindrical core sampler (surface area 0.07 m^2), which was pushed into the sediment of the *N. peltata* stands by a SCUBA diver. At each sampling date the diver harvested the macrophyte material from 5—7 cores to a depth of approximately 40 cm into the sediment. The plants from each core were placed separately in plastic bags and transported to the laboratory.

In the laboratory the living macrophyte material from each sample was cleaned of mud, associated fauna and loose periphyton by washing with tap water and gently polishing with a cloth. The *N. peltata* plants from each quadrat or core were divided into roots, short shoots, long shoots, petioles, leaf blades and reproductive structures (flowers, fruits and peduncles). The flowering stems were considered as long shoots because they are morphologically alike. The separated plant parts were then packed separately in aluminium foil, dried at 105°C for 24 h and weighed. They were then ground until sample homogeneity was assured visually. A subsample from each component was ashed at 550°C for 4 h in a muffle furnace to determine the ash-free dry weight. Mean values of biomass per m^2 of bottom area, expressed as g dry weight and g ash-free dry weight, and standard deviations were calculated for the various plant structures at each sampling date. Samples of dried, ground, and carefully weighed *N. peltata* structures were analysed for organic carbon with an Oceanography International Carbon Analyser (model 05224B-AA), modified according to Roelofs (1983).

By dividing the harvested *N. peltata* plants into their morphological structures it was possible to study the seasonal changes in each of the plant parts. On August 5, when the peak biomass of *N. peltata* was found, estimations were made of the relationship between surface area of the above-ground structures and their weight. The surface area of 50 leaf blades was measured with a planimeter (Kontron MOP-AM03). The surface area of 50 petioles and several metres of long shoots was estimated by considering these organs as cylinders and by measuring their diameter and length. By assuming the relationship between surface area and weight to be constant throughout the year the seasonal changes in above-ground surface area of *N. peltata* in m^2 per m^2 of bottom could be estimated.

In the Bemmelse Strang it was difficult to study the vertical arrangement of the *N. peltata* biomass in space and time because of the high water levels and the high turbidity of the water. Therefore, the vertical stratification of the biomass was studied in concrete tanks (length 150 cm, width 80 cm, depth 60 cm) at the university, using cultures of *N. peltata.* On several days in 1980 the arrangement of the above-ground biomass was thoroughly ex-

amined and precisely recorded before harvesting *N. peltata* from a surface area of 0.25 m^2 at the bottom—water interface; care was taken to minimize damage to the plants. The carefully cleaned and washed plants were projected on a two-dimensional plane in accordance with their natural arrangement. The roots were arranged vertically. The *N. peltata* plants were then divided into several 2.5-cm segments with razor blades, dried (105°C, 24 h) and weighed.

In the Bemmelse Strang, the development, productivity and turnover rates of the floating leaves were studied with the leaf-marking technique in permanent quadrats (see Van der Velde et al., 1984). In the present paper, the results from the permanent quadrat in the centre of the *N. peltata* stand are used to calculate leaf-blade production. A square PVC tube frame, enclosing an area of 0.25 m^2, was held approximately 15 cm under the water surface by stones, strings and cork floats so that the unrolling of floating leaves at the water surface was not hindered. Newly developed leaves in the plot were marked with aluminium strips on which a number was scratched. Observations were made twice a week so that the fate of each individual leaf which developed within the permanent quadrat could be followed. At each observation length (L) and width (W) of each leaf were measured. The surface area of each leaf blade at each date was calculated by means of the formula: $1.028\ ((L + W)/4)^2$ (Van der Velde et al., 1982). The surface area of each leaf blade was correlated with its biomass according to the regression equation $y = 3.925x - 26.572$ (y = biomass in mg ash-free dry weight; x = the area of the leaf blade in cm^2). The contribution of damage, such as the grazing by herbivores, was estimated visually as a percentage of the area per leaf blade on each date. For each observation date the potential and actual biomass of the leaf blades per m^2 water surface could be estimated in this way. The potential biomass is defined as the biomass calculated with the above-mentioned formula, while the actual biomass is the potential biomass minus the biomass grazed by herbivores. A more detailed description of the leaf-marking method is presented in Van der Velde et al. (1982, 1984).

The growth and/or mean persistence of roots, short shoots and long shoots were studied in 7 concrete tanks (length 200 cm, width 135 cm, depth 80 cm) at the university. Each concrete tank contained a layer of 10 cm river clay and a water layer of 40 cm. In natural systems short shoots with roots hibernate and form new leaves and long shoots in spring. In April, 8 short shoots (with roots) were planted in the substrate of each concrete tank. Each short shoot was measured and marked with a piece of rotex tape on which a number was printed. Each month, from May until December, the *N. peltata* plants of one concrete tank were harvested and the initially tagged short shoots and the newly formed underground plant parts were measured and examined. The development of the long shoots, which creep over the bottom and are green in colour, was examined weekly in one concrete tank. These shoots were harvested in December. It is assumed that

the roots of *N. peltata* have the same turnover rate as the short shoots and that this rate is the same in the concrete tanks and in the Bemmelse Strang.

RESULTS AND CONCLUSIONS

Seasonal changes in biomass and organic carbon content

The monthly mean values and standard deviations of the total *N. peltata* biomass per m^2 sediment surface in 1980 are presented in Fig. 1A. Biomass increase began in May and rapidly developed until August (the extension phase). A peak in biomass of 425 g dry weight (= 372 g ash-free dry weight) per m^2 was reached in August. A decrease in biomass could be observed from September until December. The hibernation phase extended from

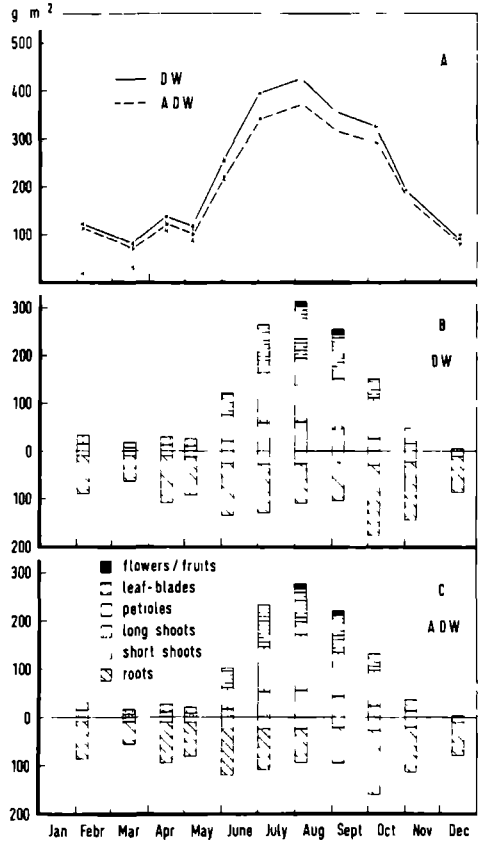


Fig. 1. (A) Total *Nymphoides peltata* biomass with standard deviations in g dry weight (D.W.) and g ash-free dry weight (A.D.W.) per m^2 sediment surface in the Bemmelse Strang at each sampling date in 1980. (B and C) Shares in g dry weight (B) and g ash-free dry weight (C) of the various plant parts of *Nymphoides peltata* per m^2 sediment surface at each sampling date and their occurrence aboveground and underground.

December to May. The seasonal changes in biomass and air and water temperature show similar tendencies; in August both the highest temperatures and the peak biomass of *N. peltata* were recorded.

In Fig. 1 B and C and Tables I and II the biomass of the different organs is presented for each sampling day. In winter and early spring 74—97% of the total biomass could be found in the sediment, while in August, when the maximum standing crop was found, 74% of the biomass occurred aboveground. The standing crops of petioles, long shoots, short shoots and roots did not differ significantly in the period February—May. After this period an increase in biomass of most organs was observed. The leaf blades and their petioles showed a more or less similar increase in biomass during the period May—August, reaching their maximum standing crops in August (27 and 31% of the peak biomass, respectively). During the declination phase, the biomass of the leaf blades disappeared more quickly than the biomass of the petioles, partly because of its higher breakdown rate (Brock et al., 1982), the grazing of leaf blades by animals and the more pronounced effect of wind and wave action on the leaf blades during the autumn storms. The increase of the long shoots (flowering stems included) particularly occurred in the period June—July, while its maximum standing crop was attained in August (15% of total). The short shoots increased in biomass very early in the growing season during the period May—June, remaining at a more or less constant level in the period June—November. The biomass of the roots showed some irregular fluctuations during the year. They were difficult to collect because these organs were anchored in the sediment up to a depth of ca. 40 cm, resulting in sampling errors. The decrease in biomass of the roots in the period July—August, however, might be attributed to the sudden increase in water level which resulted in the submergence of many leaf blades (see Fig. 4). The formation of a great number of new floating leaves most probably caused a re-allocation of organic substances from the roots towards the leaves in that period. The formation of flowers and fruits may also effect such a re-allocation; however, flowering of *N. peltata* was very minor in 1980, probably due to the high water levels. Only 3% of the biomass in September comprised the flowering structures. Furthermore, it was remarkable that during the whole sampling period no seedlings of *N. peltata* have been found.

The organic carbon content (TOC) per g dry weight is influenced by the seasonal fluctuations in ash content of the various organs and is therefore expressed as a percentage of the ash-free dry weight (AFDW) in Table III. The organic carbon content per g AFDW was rather constant throughout the year and ranged from 49 to 55% for the total macrophyte. The highest organic carbon content was found during August and September. The mean annual organic carbon content per g AFDW showed the following sequence: leaf blades > flowering structures > petioles > long shoots ≈ short shoots > roots. In August, a peak in biomass of 205 g organic carbon was found.

TABLE I

Mean biomass in g dry wt. and standard deviations (S.D.) of the various plant parts of *Nymphoides peltata* per m^2 sediment surface in the Bemmelse Strang at each sampling date in 1980

	4-II	17-III	14-IV	6-V	2-VI	2-VII	5-VIII	2-IX	30-IX	28-X	16-XII
Total biomass	123.69	81.25	139.21	117.84	254.19	394.44	425.08	357.60	326.57	193.40	90.23
±S.D.	111.80	49.81	32.84	34.78	38.25	86.42	48.95	31.13	42.95	49.28	24.40
Aboveground biomass	32.50	18.26	30.52	25.56	120.13	264.12	314.25	254.12	150.08	48.67	2.88
±S.D.	29.29	9.43	9.36	8.00	30.37	25.70	33.89	17.55	38.66	7.77	2.33
Underground biomass	91.19	62.99	108.69	92.29	134.06	130.33	110.83	103.47	176.48	144.74	87.35
±S.D.	82.51	42.69	24.93	31.78	22.43	68.86	19.55	32.12	42.89	41.99	24.46
Flowers/fruits	—	—	—	—	—	—	6.89	10.94	0.43	—	—
±S.D.	—	—	—	—	—	—	4.63	11.64	0.40	—	—
Leaf blades	—	0.08	0.09	0.23	44.81	99.35	113.98	91.76	38.29	0.35	—
±S.D.	—	0.05	0.06	0.12	14.95	13.15	11.41	7.59	18.16	0.21	—
Petioles	16.75	10.27	18.48	16.56	55.42	106.58	132.86	105.12	85.38	33.20	0.16
±S.D.	22.38	6.33	2.91	5.98	15.31	24.17	22.02	5.37	18.41	10.02	0.15
Long shoots	15.75	7.91	11.96	8.76	19.90	58.19	60.53	46.30	25.99	15.13	2.72
±S.D.	6.91	3.49	6.59	6.50	1.99	15.77	12.99	12.26	8.82	2.45	2.43
Short shoots	9.20	9.54	11.73	13.11	27.04	28.28	26.67	23.96	29.79	23.17	11.22
±S.D.	9.04	6.01	3.40	4.30	3.30	15.61	9.17	10 36	15.77	5.82	4.49
Roots	81.99	53.41	96.95	79.18	107.02	102.05	84.16	79.51	146.70	121.57	76.13
±S.D.	73.46	37.10	22.87	28.40	19.42	53.36	12.81	29.13	38.95	36.17	23.03

TABLE II

Mean biomass in g ash-free dry wt. and standard deviations (S.D.) of the various plant parts of *Nymphoides peltata* per m^2 sediment surface in the Bemmelse Strang at each sampling day in 1980

	4-II	17-III	14-IV	6-V	2-VI	2-VII	5-VIII	2-IX	30-IX	28-X	16-XII
Total biomass	117.18	71.41	122.89	101.90	221.94	341.86	372.18	317.54	292.34	173.13	81.58
±S.D.	106.56	38.98	32.29	30.42	39.95	75.10	37.68	29.25	35.11	37.74	22.10
Aboveground biomass	30.13	16.36	27.21	20.04	101.26	232.70	277.11	221.65	131.67	40.44	2.50
±S.D.	26.81	8.60	8.11	6.93	28.18	22.64	29.23	16.14	34.02	4.90	2.23
Underground biomass	87.05	55.05	95.68	81.87	120.68	109.09	95.06	95.89	160.67	132.69	79.08
±S.D.	78.75	37.19	25.59	28.45	20.01	57.64	17.72	29.75	39.49	33.12	22.13
Flowers/fruits	—	—	—	—	—	—	6.23	9.89	0.39	—	—
±S.D.	—	—	—	—	—	—	4.19	10.52	0.36	—	—
Leaf blades	—	0.07	0.07	0.19	39.42	85.83	98.03	76.20	33.42	0.28	—
±S.D.	—	0.04	0.04	0.10	14.20	11.36	9.81	5.10	15.85	0.16	—
Petioles	15.04	9.18	15.99	11.96	45.48	93.90	116.85	93.32	73.88	26.16	0.15
±S.D.	20.14	5.69	2.28	4.81	13.17	21.29	19.36	4.77	15.93	6.92	0.14
Long shoots	15.09	7.11	11.15	7.88	16.35	52.79	55.54	42.24	23.97	14.00	2.35
±S.D.	6.67	3.20	6.19	5.91	3.56	14.30	11.92	11.18	8.14	2.18	2.10
Short shoots	8.71	8.86	11.04	11.25	25.11	24.94	24.80	21.93	27.84	21.37	10.23
±S.D.	8.56	5.68	3.29	4.22	3.07	13.77	8.53	9.48	14.73	5.21	4.10
Roots	78.19	46.20	84.63	70.61	95.57	84.40	70.73	73.96	132.84	111.32	68.85
±S.D.	70.19	31.73	23.63	24.92	17.38	44.13	10.77	27.09	34.72	27.91	20.83

TABLE III

The percentages of organic carbon per g ash-free dry wt. of the various plant parts of *N. peltata* in the Bemmelse Strang at each sampling date in 1980

	4-II	17-III	14-IV	6-V	2-VI	2-VII
Flowers/fruit	—	—	—	—	—	—
Leaf blades	—	—	—	—	59	55
Petioles	49	49	50	58	54	53
Long shoots	48	54	49	51	52	50
Short shoots	48	53	52	53	52	51
Roots	49	54	48	50	50	50
Total macrophyte	49	53	49	51	53	52

The vertical stratification of the biomass

During all seasons a large proportion of the *N. peltata* biomass was present just above and below the sediment surface (Fig. 2). The long shoots (stolons) and short shoots (root stocks) were responsible for this. Because the root biomass decreased with sediment depth, it was greatest in the upper 10 cm. In spring and autumn a small proportion of the biomass was found in several layers of the water column. Short petioles or remnants of decaying petioles were responsible for this. In summer a large amount of biomass, mainly leaf blades, was found at the water surface. A relatively large portion of biomass was also located just below the water surface in August (fruits and the upper parts of the petioles and the flowering stems). In August, only a small proportion of the biomass was present in the middle part of the water column; here the petioles and flowering stems were arranged more or less vertical, while in the upper layers of the water column the arrangement was more or less horizontal. We also observed that most of the flexible petioles of *N. peltata* were spirally twisted, giving each other support to withstand wind and wave action. The petioles, which originated from the short shoots and long shoots near the sediment surface, were mostly longer than the depth of the water column. In this way minor fluctuations in water level could occur without causing the leaf blades to disappear under water. Sudden, larger fluctuations in water level, however, can result in the drowning of the leaf blades. Only the petioles of the younger leaves retain the capacity to elongate, allowing its leaf blades to reach the water surface, while the older leaves ultimately decompose.

Seasonal changes in above-ground surface area

In August, 1 g AFDW of leaf blades corresponded with an area of 0.0252 m^2, measured on one side of the leaf blades. According to Van der Velde et al. (1979) the relationship of weight and surface area is constant for the

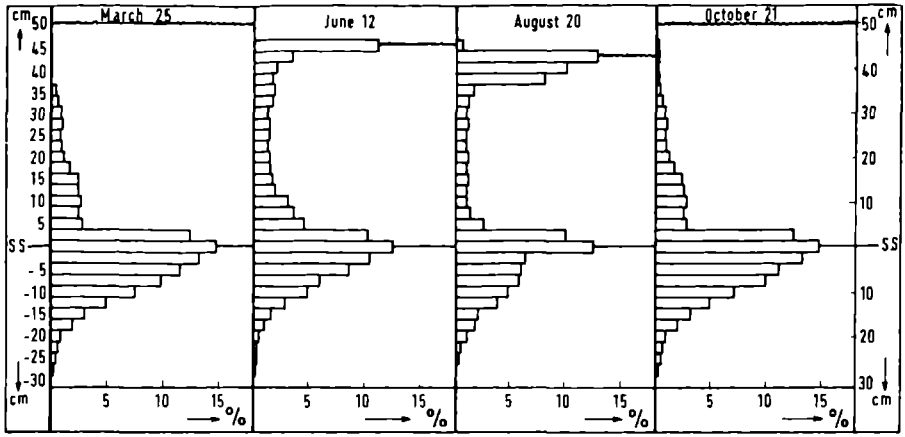
5-VIII	2-IX	30-IX	28-X	16-XII
57	56	54	—	—
57	61	55	44	—
56	55	52	53	48
53	52	51	50	49
51	53	51	51	50
53	50	51	49	49
55	55	51	50	49

leaf blades of *N. peltata*. This conversion factor can be used to calculate the leaf area index (LAI) from the seasonal changes in biomass. Only one side of the leaf was used to calculate the LAI because during the growing season most leaves of *N. peltata* occur floating at the water surface so that it can be assumed that the upper surface of the leaf blade is particularly important for the macrophyte with respect to light absorption and photosynthesis. Furthermore, the area calculated is available for both terrestrial (upper part of leaf blades) and aquatic organisms (lower side). It is important to remember, however, that the leaf blades considerably overlapped each other at the water surface and that parts of the leaf blades could be in a more or less senescent state. Furthermore, the young leaves which grow towards the water surface, are completely submerged so that the leaf area index calculated in this way does not occur completely at the water surface (see Van der Velde et al., 1984 for a detailed description of the LAI of *N. peltata* at the water surface).

In August, 1 g AFDW of petioles and long shoots corresponded with a surface area of 0.0233 and 0.0148 m^2, respectively. We calculated the seasonal changes in area index of petioles and long shoots from their seasonal changes in biomass by assuming that the relationship between weight and surface area of these organs was constant throughout the year. In August, the leaf blades, petioles and long shoots had a maximum surface area of 2.51, 2.72 and 0.82 m^2, respectively, which totalled 6.05 m^2 per m^2 of bottom surface for above-ground biomass (Fig. 3). The calculated plant surface area must be considered as only theoretically available for aquatic macro-invertebrates and periphytic organisms.

Annual net productivity

The annual turnover rate of the leaf blades of *N. peltata* was estimated from the results of work done in the permanent quadrat in the centre of the *N. peltata* belt (Fig. 4). The development and fate of each leaf blade



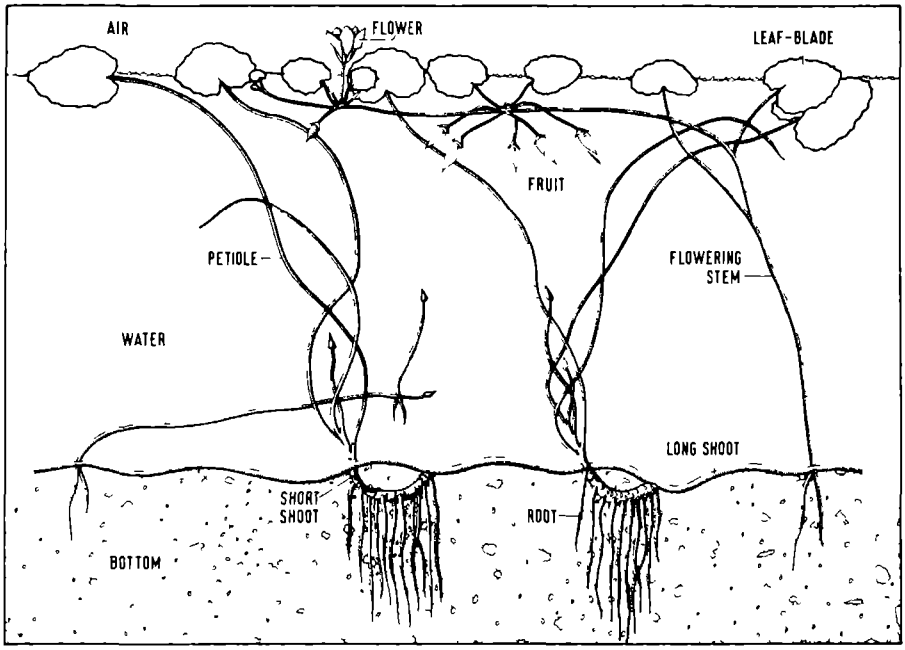


Fig. 2. (Above) Seasonal changes in the vertical stratification of the relative biomass of *Nymphoides peltata*, above and below the sediment surface (S.S.) in a concrete tank. (Below) General architecture of *Nymphoides peltata* at the time of its peak biomass.

was followed throughout the growing season of 1980 (see also Van der Velde et al., 1984). The length of the vegetation period was 169 days, beginning with the first leaf emergence within the permanent quadrat and ending on the day the last leaves disappeared. The mean leaf blade persistence was calculated to be 23.14 days. The average actual biomass of the leaf blades in the permanent quadrat was 26.35 g AFDW per m^2 water

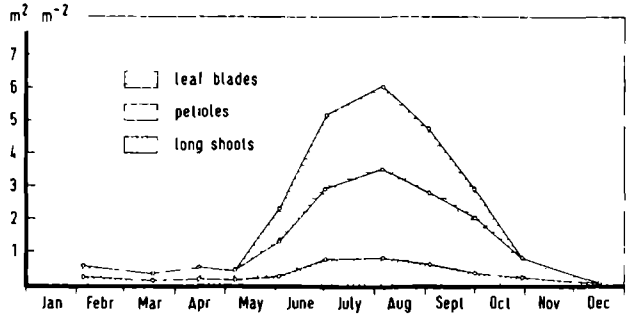


Fig. 3. Surface area in m^2 of the submerged above-ground plant parts of *Nymphoides peltata* per m^2 sediment surface in the Bemmelse Strang at each sampling date in 1980.

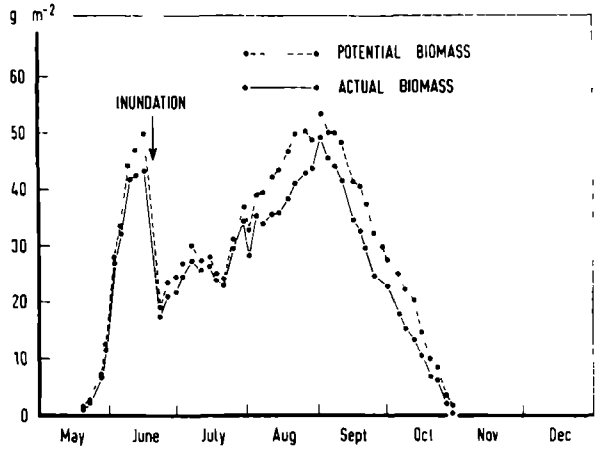


Fig. 4. Seasonal changes in actual and potential leaf-blade biomass of *Nymphoides peltata* in g ash-free dry weight as measured in a permanent quadrat in the centre of the *Nymphoides peltata* belt in the Bemmelse Strang.

surface, while the average potential biomass was 30.56 g AFDW per m^2. The annual leaf-blade production in the permanent plot (Van der Velde et al., 1984) appeared to be 228.00 g AFDW per m^2 water surface. Their productivity estimate cannot be used in our study because the seasonal changes in biomass in our study are expressed per unit area of sediment surface, while the seasonal changes in biomass within the permanent quadrat are expressed per unit area of water surface. The floating leaves, which were anchored within 1 m^2 at the sediment surface, mostly occupied a larger area at the water surface. Thus, mostly higher amounts of leaf-blade biomass were obtained with the harvest method than with the permanent quadrat method. Furthermore, at each sampling date the leaf blades were harvested from four sites in the centre of the *N. peltata* belt, while only one permanent quadrat was located there. It is assumed, however, that the turnover rate of the leaf blades from the permanent quadrat can be used to calculate the an-

nual net productivity of the leaf blades that were harvested. From the results of the permanent quadrat three turnover rates can be calculated

$$(A)\ \frac{\text{length of the vegetation period}}{\text{mean leaf-blade persistence}} = \frac{169}{23.14} = 7.30$$

$$(B)\ \frac{\text{annual leaf-blade production}}{\text{average potential biomass of leaf blades}} = \frac{228.0}{30.56} = 7.46$$

$$(C)\ \frac{\text{annual leaf-blade production}}{\text{average actual biomass of leaf blades}} = \frac{228.0}{26.35} = 8.65$$

It seems that turnover rate A and turnover rate B, in which grazing of leaf blades is ignored, are very much alike, while turnover rate C, in which grazing of leaf blades is taken into account, differs considerably from the others.

The annual net productivity of the leaf blades per m^2 sediment surface can be estimated by multiplying their average standing crop for the growing season by turnover rate C. In the present study turnover rate C (8.65) is used to calculate annual leaf-blade production because with the harvest method the actual standing crop per date is determined. The average standing crop for the growing season was estimated as follows: at first the mean leaf-blade biomass per m^2 bottom surface was calculated for the intervals 6 May—2 June, 2 June—2 July, 2 July—5 August, 5 August—2 September, 2 September—30 September and 30 September—28 October, then the mean leaf-blade standing crop was calculated from these data, being 64.75 g dry weight (55.53 g AFDW and 32.06 g TOC). By multiplying these data with the turnover rate (8.65) the annual primary productivity for the leaf blades was estimated to be 560.09 g dry weight (480.33 g AFDW and 277.32 g TOC) per m^2 bottom surface.

According to Brock et al. (1982) the petioles of *N. peltata* decompose at a slower rate than the leaf blades. By comparing the half-lives of petioles and leaf blades the mean petiole persistence was estimated to be 28.93 days. The turnover rate of the petioles can be calculated as follows

$$\text{turnover rate} = \frac{\text{length of the vegetation period}}{\text{mean petiole persistence}} = \frac{169}{28.93} = 5.84$$

Grazing of petiole biomass by macrofauna was very minor in the Bemmelse Strang, so the actual harvested biomass of the petioles was nearly equal to the potential biomass (as defined above). Therefore, the annual net productivity of the petioles per m^2 sediment surface can be estimated by multiplying the average petiole standing crop during the vegetation period by 5.84. The mean petiole biomass for the intervals as given above was 85.04 g dry weight (73.75 g AFDW and 39.99 g TOC) per m^2. By multiplying these data with the turnover rate (5.84), the annual primary productivity for the petioles was estimated to be 496.63 g dry weight (430.70 g AFDW and 233.54 g TOC) per m^2 bottom surface.

Weekly observations on the development of the long shoots in the concrete tanks showed that in the period May—August the long shoot biomass increased, while there were no or few losses due to grazing or decomposition. After flowering of *N. peltata* the standing crop of the long shoots did not increase any more, but gradually decreased due to senescence and microbial breakdown. Also in the Bemmelse Strang grazing or decomposition of the long shoots normally did not occur in the quadrats which were harvested in the period May—August. However, at some localities long shoots could become uprooted by the activities of waterfowl or muskrats in this period. The annual net productivity of the long shoots in the Bemmelse Strang was estimated to be 51.77 g dry weight (47.66 g AFDW and 25.41 g TOC) per m^2 bottom surface (the increase in biomass for the period). The increase of the biomass of the flowering structures in the period July—September was also considered as annual net production, being 10.94 g dry weight (9.89 g AFDW and 5.54 g TOC) per m^2.

The turnover rate of the short shoots was estimated by studying their annual length increase. The short shoots, which were planted in the concrete tanks in April had a length of 3.7 ± 1.2 cm. The most conspicuous length increase of these short shoots occurred in the period May—July; this organ reached a length of 7.8 ± 2.9 cm. In the period May—July, the production of new short shoots, which had not been planted before, reached a length of 4.0 ± 2.0 cm. Several of the short shoots initially planted had disappeared when *N. peltata* was harvested from the last concrete tank in December, while several other tagged short shoots were in a senescent state. On the other hand the newly-formed short shoots of that year had a healthy appearance then. Although these data are preliminary it is assumed that new short shoots are formed in spring and early summer, reaching a length of approximately 3—5 cm that same growing season. These short shoots hibernate and their growth starts again in spring and early summer, reaching a length of approximately 6—10 cm; these hibernated short shoots also form new leaves and long shoots in spring and the long shoots in their turn can form the new short shoots. The short shoots which hibernated apparently die off in the end of the second growing season, while the newly formed short shoots hibernate. These observations are in agreement with those of Van der Velde et al. (1979) who observed that the longest short shoots were found in spring and summer, while in autumn and winter shorter short shoots were found. The mean persistence of the short shoots was estimated to be 18 months, giving a turnover rate of 0.67. By multiplying the average biomass of the short shoots in 1980 with this turnover rate, the annual net productivity was estimated to be 13.02 g dry weight (11.94 g AFDW and 6.14 g TOC) per m^2 sediment surface. The majority of the roots of *N. peltata* are connected to the short shoots. It is assumed that the roots of *N. peltata* have the same turnover rate as the short shoots. The annual net productivity of the roots can be estimated by multiplying the average root biomass in 1980 by 0.67, being 62.66 g dry weight (55.87 g AFDW and 28.00 g TOC) per m^2 bottom surface.

The total annual net production of *N. peltata* per m^2 sediment surface was estimated to be 1195.11 g dry weight, 1036.39 g AFDW and 575.95 g TOC, respectively. In Table IV the annual productivity estimates of the various morphological structures are presented. From these data it appears that the leaf blades and their petioles contributed most to the production.

TABLE IV

The estimated annual net production in g dry wt., g ash-free dry wt. and g organic carbon of the various plant parts of *Nymphoides peltata* per m^2 sediment surface in the Bemmelse Strang in 1980

	Dry weight	Ash-free dry weight	Organic carbon
Flowers/fruits	10.94	9.89	5.54
Leaf blades	560.09	480.33	277.32
Petioles	496.63	430.70	233.54
Long shoots	51.77	47.66	25.41
Short shoots	13.02	11.94	6.14
Roots	62.66	55.87	28.00
Above-ground	1119.43	968.58	541.81
Underground	75.68	67.81	34.14
Total	1195.11	1036.39	575.95

DISCUSSION

In examining Table V, it appears that the amount of plant surface area available for colonization by periphyton and aquatic macro-invertebrates can be high but varies greatly between species. The maximum submerged surface area supplied by *N. peltata* in the Bemmelse Strang is intermediate between those reported for emergent and submerged macrophytes (Table V). This phenomenon at least partly can be explained by the nymphaeid growth form of the studied macrophyte. Also the peak biomass values of macrophytes vary greatly between species (Whigham et al., 1978). The peak biomass value of *N. peltata* as found in the present study is intermediate in the reported range for nymphaeids (Table VI). The low above-ground biomass of *N. peltata*, as found by Van der Velde et al. (1979) in the Bemmelse Strang, must be attributed to the prolonged drought during their sampling period, so that the proportion of the underground organs was relatively large. When compared with other nymphaeids it appears that *N. peltata* has a relatively low percentage of its peak biomass belowground (Table VI).

Nymphoides peltata can be considered as a nymphaeid species with more or less typical pioneer characteristics. By means of vegetative propagation with the long shoots, *N. peltata* has the potential to colonize large areas

TABLE V

Reported maximum surface areas, in m^2, of the submerged above-ground plant parts of some aquatic macrophytes per m^2 of littoral

Source	Species	Area
	Emerged macrophytes	
Pieczynska and Ozimek (1976)	*Phragmites australis* (Cav.) Trin. ex Steud.	2.0
Pieczynski (1977)	*Schoenoplectus lacustris* Palla	2.1
Allen (1971)	*Scirpus acutus* Muhlenberg	0.5
	Floating leaved macrophyte	
This study	*Nymphoides peltata*	6.1
	Submerged macrophytes	
Pieczynska and Ozimek (1976)	*Potamogeton perfoliatus* L.	11.5
Pieczynska and Ozimek (1976)	*Potamogeton lucens* L.	15.6
Odum (1957)	*Sagittaria lorata* (Chapm.) Small	24.3
Pieczynska and Ozimek (1976)	*Myriophyllum spicatum* L.	29.6
Pieczynska and Ozimek (1976)	*Elodea canadensis* Michx	37.8

within one growing season. The colonization of area by other nymphaeids, such as *Nuphar lutea* (L.) Sm. and *Nymphaea alba* L. is much slower, because these species do not possess stolons; however, they invest more in their underground biomass. The presence of *Nymphoides* in former river beds which are flooded by river water in winter and early spring (see also Van der Voo and Westhoff, 1961) may be partly explained by the species pioneering characteristics; during periods of flooding suitable circumstances for colonization can be created because of sedimentation of new clay or the washing away of the upper detritus layer. It appeared during our investigations, however, that unpredictable rises in water level during the growing season diminish the vitality of *Nymphoides* (Fig. 4).

In the Bemmelse Strang the P/B max. ratio of *N. peltata* was 2.8 for the total macrophyte and 3.6 for the above-ground parts. Information on P/B max. ratios of other nymphaeids is scarce. From results presented by Blanton (1976) the P/B max. ratio of *Nuphar advena* can be calculated as 1.3 for the total plant and 3.5 for the above-ground parts. Also, when compared with other freshwater macrophytes (see Westlake, 1982), it can be concluded that *Nymphoides peltata* has a high P/B max. ratio. A high P/B max. ratio of a macrophyte is the result of rapid turnover rates of all or some of its organs. Van der Velde (1980) compared the turnover rates of the floating leaves of several nymphaeids which occur in The Netherlands *viz.*, *Nymphaea alba*, *Nymphaea candida* Presl, *Nuphar lutea* and *Nymphoides peltata*. It appears that among these *N. peltata* had the highest turnover rate. Because of the higher turnover rate of the floating leaves and the relatively small proportion of its biomass underground (Table VI), *N. peltata* probably has a higher P/B max. ratio then the other nymphaeid species studied by Van der Velde (1980).

TABLE VI

Reported peak biomass values in g dry wt. of some nymphaeid water plants and the percentages occurring underground

Source	Location	Species	Total	Above-ground	Under-ground
Waring (1970)	Pennsylvania	*Nuphar advena*	1329	253	1076 (81%)
Good and Good (1975)	New Jersey	*Nuphar advena*	1751	605	1146 (65%)
Blanton (1976)	North Carolina	*Nuphar advena**	179	53	126 (70%)
Eriksson (1973)	Sweden	*Nuphar lutea*	193	33	160 (83%)
Bernatowicz and Pieczynska (1965)	Poland	*Nuphar lutea*	—	192	—
Esteves (1979)	Germany	*Nuphar lutea*	—	405	—
Bernatowicz and Pieczynska (1965)	Poland	*Nymphaea alba*	—	321	—
Esteves (1979)	Germany	*Nymphaea alba*	—	293	—
Smart (1980)	Wisconsin	*Nymphaea tuberosa* Paine	850	512	338 (40%)
Van der Velde et al. (1979)	The Netherlands	*Nymphoides peltata*	287	157	130 (45%)
This study	The Netherlands	*Nymphoides peltata*	425	314	111 (26%)
Ikusima (1970)	Japan	*Nymphoides peltata*	270**	194	76 (28%)
Esteves (1979)	Germany	*Polygonum amphibium* L.	—	167	—

*Reported as *Nuphar luteum* (L.) Sibthorpe & Smith.
**Not clear whether peak biomass value is given.

In the present study the annual net productivity of several organs was estimated by multiplying the average standing crops of these organs by their turnover rate. The turnover rate of the underground biomass of *N. peltata* could not be determined by tagging short shoots in the Bemmelse Strang because of high water levels, a high turbidity of the water and the density of the vegetation. Therefore the turnover rate of the underground biomass was determined from cultures in concrete tanks. It may be argued that the growth of underground plant parts is sensitive to ambient environmental conditions and stand density of the underground parts, so that data obtained from cultures are not applicable to the field situation. Stand density particularly of the underground plant parts was much lower in the concrete tanks than in the field. This may have caused the elimination of competition and, consequently, a better growth and a longer persistence of the underground plant parts in the concrete tanks. In the present study the annual underground production was estimated to be ca. 7% of the total annual production. This might be an underestimate because the turnover rate of the underground plant parts is probably higher in the Bemmelse Strang than in the concrete tanks.

Another deficiency of our production estimate is that organic losses due to secretion from growing tissues of *N. peltata* have not been measured. The loss of excreted organic carbon from macrophytes is in part correlated with photosynthetic activity (Hough and Wetzel, 1975). Wetzel et al. (1972) approximate the excreted organic carbon from macrophytes to be ca. 4% of the photosynthetic production.

According to Westlake (1982) determinations of production from biomass changes must take into account the translocation of organic matter. In nature, individual organs die gradually when still connected to the plant. Under these circumstances, the quality of the senescent organ might be affected by resorption and translocation of organic matter. If productivity is estimated with turnover rates and translocation is occurring it is easy to overestimate production because the organic matter that is withdrawn from one floating leaf can be used to initiate the growth of another. The floating leaves of *N. peltata* continually emerge and die off throughout the growing season. In this study the resorption of organic matter prior to senescence of the floating leaves was not measured and will probably be very difficult to measure. Thus, our productivity estimate probably implies an overestimation of the above-ground production of *N. peltata.*

Ideally, the production methodology chosen should be accurate and precise. Primary production is the amount of new organic matter formed by photosynthesis and thus, theoretically, can be estimated by measuring the changes in oxygen concentrations or inorganic carbon uptake in a chamber enclosing the macrophytes. However, since Hartman and Brown (1967) demonstrated that the oxygen produced by photosynthesis can be stored and recycled in the internal lacunar system of macrophytes, the oxygen method must be considered as questionable; *N. peltata* has a well developed

lacunar system. According to Hough (1974) refixation of respired CO_2 may also be extensive in aquatic plants. Furthermore, the complex structure of *N. peltata* probably enables the plant to exchange oxygen and inorganic carbon from the air, water and sediment. According to Filbin (1980) inorganic carbon from both the atmospheric and aqueous phase is a significant source of carbon for photosynthesis in floating-leaved macrophytes. Dacey (1981) demonstrated the existence of a ventilation system in a nymphaeid water plant in which a flux of air down the petioles of the youngest leaves forced a simultaneous efflux of CO_2-enriched gas from the rhizome towards the older leaves. Recent studies using $^{14}CO_2$ (Wium-Andersen, 1971; Sønder-gaard and Sand-Jensen, 1979) have shown that some water plants fix significant quantities of sediment-derived CO_2. This source of inorganic carbon might be significant in the productivity of nymphaeids and, thus, may represent wrong estimates of carbon fixation. In most studies on nymphaeids only the photosynthetic capacity of the leaf blades was investigated. However, other green parts have a large share in biomass and can photosynthesize also. Furthermore, floating leaves which cover the water surface are mostly arranged in a mosaic pattern with a certain amount of overlap. According to Ikusima (1970) the rate of photosynthesis of the first and uppermost layer of leaves exposed to direct sunshine is higher than that of the second layer of floating leaves, etc., because they receive weaker light filtered by the upper leaf blades. In fact more basic information concerning the photosynthesis and the inorganic carbon uptake by all organs of nymphaeids in their natural systems is necessary before a reliable net primary productivity can be established in this way.

It is our opinion that no single method can give definite productivity estimates of nymphaeids in natural systems. Investigations measuring photosynthesis are theoretically likely to give the most complete estimates of production. However, they are technically very difficult for nymphaeids and imply short-term experiments. The method used in this study is pragmatically and financially feasible and corrects for rapidly changing environmental conditions, since it involves the whole vegetation period. Growth modelling, in which photosynthesis and respiration measurements are combined with traditional productivity estimates (Best, 1982) perhaps will make it possible to come to a more or less definite crop simulation of nymphaeids under natural circumstances.

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REFERENCES

Allen, H.L., 1971. Primary productivity, chemo-organotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. Ecol. Monogr., 41: 97—127.

Bernatowicz, S. and Pieczynska, E., 1965. Organic matter production of macrophytes in the lake Taltowisko (Mazurian Lakeland). Ekol. Pol. (Ser. A), 13: 113—124.

Best, E.P.H., 1982. Growth modelling in aquatic macrophytes. In: J.J. Symoens, S.S. Hooper and P. Compère (Editors), Studies on Aquatic Vascular Plants. Royal Botanical Society of Belgium, Brussels, pp. 102—111.

Blanton, L.R., 1976. Primary productivity and biomass distribution. In: M.M. Brinson and G.J. Davis (Editors), Primary Productivity and Mineral Cycling in Aquatic Macrophyte Communities of the Chowan River, North Carolina. Water Res. Resour. Inst. (Univ. N. Carolina). Report no. 120, 173 pp.

Brock, Th.C.M., Huijbregts, C.A.M., van de Steeg-Huberts, M.J.H.A. and Vlassak, M.A., 1982. In situ studies on the breakdown of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae); some methodological aspects of the litter bag technique. Hydrobiol. Bull. (Amsterdam), 16: 35—49.

Dacey, J.W.H., 1981. Pressurized ventilation in the yellow water lily. Ecology, 62: 1137—1147.

Den Hartog, C., 1978. Structural and functional aspects of macrophyte-dominated aquatic systems. In: Proc. European Weed Research Society, 5th Symposium on Aquatic Weeds, Amsterdam, pp. 35—41.

Den Hartog, C., 1982. Architecture of macrophyte-dominated aquatic communities. In: J.J. Symoens, S.S. Hooper and P. Compère (Editors), Studies on Aquatic Vascular Plants. Royal Botanical Society of Belgium, Brussels, pp. 222—234.

Den Hartog, C. and Segal, S., 1964. A new classification of the water-plant communities. Acta Bot. Neerl., 13: 367—393.

Erikson, F., 1973. Makrofyterna och deras produktion i sjön Vitalampa (Klotenprojectet Rapport no. 2). Scr. Limnol. Upsal., 346: 1—36.

Esteves, F., 1979. Die Bedeutung der aquatischen Makrophyten für den Stoffhaushalt des Schöhsees. I. Die Production an Biomasse. Arch. Hydrobiol., 57: 117—143.

Filbin, G.E., 1980. Photosynthesis, photorespiration and primary productivity in floatin, floating leaved and emergent plants. Ph.D. Thesis, Wayne State University Detroit, MI, 252 pp.

Good, R.E. and Good, N.F., 1975. Vegetation of the Woodbury Creek—Hessian Run freshwater tidal marshes. Bartonia, 43: 38—45.

Hartman, R.T. and Brown, D.L., 1967. Changes in the composition of the internal atmosphere of submerged vascular hydrophytes in relation to photsynthesis. Ecology, 48: 252—258.

Hough, R.A., 1974. Photorespiration and productivity in submersed aquatic vascular plants. Limnol. Oceanogr., 19: 912—927.

Hough, R.A. and Wetzel, R.G., 1975. The release of dissolved organic carbon from submersed aquatic macrophytes: diel, seasonal, and community relationships. Verh. Int. Verein. Theor. Angew. Limnol., 19: 939—948.

Hutchinson, G.E., 1975. A Treatise of Limnology. III. Limnological Botany. New York. NY, 660 pp.

Ikusima, I., 1970. Ecological studies on the productivity of aquatic plant communities. IV. Light conditions and community photosynthetic production. Bot. Mag., 83: 330—341.

Jacobs, R.P.W.M., 1979. Distribution and aspects of production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. Aquat. Bot., 7: 151—172.

Lammens, E.H.R.R. and Van der Velde, G., 1978. Observations on the decomposition of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae) with special regard to the leaves. Aquat. Bot., 4: 331—346.

Nienhuis, P.H. and De Bree, B.H.H., 1980. Production and growth dynamics of eelgrass (*Zostera marina*) in brackish lake Grevelingen (The Netherlands). Neth. J. Sea Res., 14: 102—118.

Odum, H.T., 1957. Trophic structure and productivity of Silver Springs, Florida. Ecol. Monogr., 27: 55—112.

Petersen, C.G.J., 1913. Om Baendeltangens (*Zostera marina*) Aarsproduktion i de danske Farvande. Mindeskr. Japetus Steenstrups Fødds., 9: 1—20.

Pieczynska, E. and Ozimek, T., 1976. Ecological significance of lake macrophytes. Int. J. Ecol. Environ. Sci., 2: 115—128.

Pieczynski, E., 1977. Numbers and biomass of the littoral fauna in Mikolajskie lake and in other Masurian lakes. Ekologia Polska (Seria A), 25: 45—57.

Roelofs, J.G.M., 1983. An instrumental method for the estimation of organic carbon in seston, macrophytes and sediments. Aquat. Bot., 16: 391—397.

Smart, M.M., 1980. Annual changes of nitrogen and phosphorus in two aquatic macrophytes (*Nymphaea tuberosa* and *Ceratophyllum demersum*). Hydrobiologia, 70: 31—35.

Søndergaard, M. and Sand-Jensen, K., 1979. Carbon uptake by leaves and roots in *Litorella uniflora*. Aquat. Bot., 6: 1—12.

Van der Velde, G., 1980. Studies in nymphaeid-dominated systems with special emphasis on those dominated by *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Thesis, Catholic University, Nijmegen, 163 pp.

Van der Velde, G., Giesen, Th.G. and Van der Heijden, L., 1979. Structure, biomass and seasonal changes in biomass of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae), a preliminary study. Aquat. Bot., 7: 279—300.

Van der Velde, G., Van der Heijden, L.A., Van Grunsven, P.A.J. and Bexkens, P.M.M., 1982. Initial decomposition of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae), as studied by the leaf-marking method. Hydrobiol. Bull. (Amsterdam), 16: 51—60.

Van der Velde, G., Van der Heijden, L.A, Van Grunsven, P.A.J. and Bexkens, P.M.M., 1984. Development and productivity of the floating leaves of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Aquat. Bot., submitted.

Van der Voo, E.E. and Westhoff, V., 1961. An autecological study of some limnophytes in the area of the large rivers. Wentia, 5: 163—258.

Waring, T.G., 1970. Primary production of the emergent hydrophyte, *Nuphar advena*. Ph.D. Thesis, University of Pittsburgh, PA, 234 pp.

Westlake, D.F., 1969. Macrophytes. In: R.A. Vollenweider (Editor), A Manual on Methods for Measuring Primary Production in Aquatic Environments. IBP Handbook, 12: 25—32.

Westlake, D.F., 1982. The primary productivity of water plants. In: J.J. Symoens, S.S. Hooper and P. Compère (Editors), Studies on Aquatic Vascular Plants, Royal Botanical Society of Belgium, Brussels, pp. 165—180.

Wetzel, R.G., Rich, P.H. and Allen, H.L., 1972. Metabolism of dissolved and particulate detrital carbon in a temporate hard-water lake. Mem. Ist. Ital. Idrobiol., 29: 185—243.

Whigham, D.F., McCormick, J., Good, R.E. and Simpson, R.L., 1978. Biomass and primary production in freshwater tidal wetlands of the middle Atlantic coast. In: R.E. Good, D.F. Whigham and R.L. Simpson (Editors), Freshwater Wetlands. Academic Press, New York, pp. 3—20.

Wium-Andersen, S., 1971. Photosynthetic uptake of free CO_2 by the roots of *Lobelia dortmanna*. Physiol. Plant., 25: 245—248.

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NITROGEN AND PHOSPHORUS ACCUMULATION AND CYCLING BY *NYMPHOIDES PELTATA* (GMEL.) O. KUNTZE (MENYANTHACEAE)*

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ABSTRACT

Brock, Th.C.M., Bongaerts, M.C.M., Heijnen, G.J.M.A. and Heijthuijsen, J.H.F.G., 1983. Nitrogen and phosphorus accumulation and cycling by *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). *Aquat. Bot.*, 17: 189—214.

In 1980, the seasonal changes in nitrogen and phosphorus concentration of various plant parts of *Nymphoides peltata* (Gmel.) O. Kuntze, together with aspects of nitrogen and phosphorus cycling by this species were studied in an oxbow lake of the river Waal (The Netherlands). The nitrogen and phosphorus stores of the water, seston, sediment and macrophyte compartments were assessed each month.

The underground *Nymphoides* structures had high nitrogen and phosphorus concentrations before and after the main growing season, while during summer the aboveground plant parts had high nutrient contents. *Nymphoides peltata* accumulated maximum amounts of nitrogen (334 mmol m^{-2}) and phosphorus (56.6 mmol m^{-2}) in July. The upper layers of the bottom appeared to be an enormous nutrient reservoir (94—99% of total) of which the largest part was not directly available to *Nymphoides*. Nutrient uptake from the sediments by *N. peltata* is suggested by the fact that the bottom and/or interstitial water of the sample station devoid of rooted macrophytes, contained higher concentrations of nitrogen and phosphorus than that of the *Nymphoides* stands. The annual flux of nutrients from *Nymphoides* to the detritus compartment was estimated to be ca. 1200 mmol nitrogen and 164 mmol phosphorus per m^2 of littoral. During breakdown of the detritus there was a relatively fast net conversion of organically bound nitrogen and phosphorus to inorganic forms, especially at higher temperatures.

Nymphoides has the potential to function as an important nitrogen and phosphorus pump, which regenerates sediment nutrients.

INTRODUCTION

Among the important properties of macrophytes is their ability to accumulate nitrogen and phosphorus and their ability to accelerate nutrient turnover in aquatic systems. Nitrogen and phosphorus are essential nu-

*Contribution No. 27 of the nymphaeid project.

trients for the growth and maintenance of macrophytes and other organisms. Much attention has been given to the elemental composition of macrophytes (e.g., Hutchinson, 1975; Dykyjová, 1979, and literature cited therein). These studies indicate that the nutrient content of vascular aquatic plants is variable and depends on species, plant part, environment, time of the year and age of the plant. These studies also suggest that periodic nitrogen and phosphorus analyses of macrophytes can reveal growth strategies of water plants that involve nutrient uptake and storage. Regular nitrogen and phosphorus analyses of the various plant parts, combined with data on their biomass and turnover rates, can provide a rough approximation of the annual flux of these nutrients from the macrophyte to the detritus compartment (see Twilley, 1976). Furthermore, studying the nitrogen and phosphorus release during macrophyte breakdown is important to understand the role of macrophytes in nutrient cycling (Nichols and Keeney, 1973; Kistritz, 1978; Carpenter, 1980; Landers, 1982). When the seasonal changes in nitrogen and phosphorus content of the various environmental compartments are also studied, insight can be gained in the role of macrophytes in the nutrient balance of the whole system (Howard-Williams and Allanson, 1981; Sarvala et al., 1982; Van Vierssen, 1982).

In 1980 and 1981, the structure and aspects of production, consumption, decomposition and nutrient cycling of *Nymphoides peltata* (Gmel.) O. Kuntze were studied quantitatively in the Bemmelse Strang, an oxbow lake of the river Waal situated in the surroundings of Nijmegen (The Netherlands). The general scope of this research project, the topographical features of the study site, and the development and turnover rates of the floating leaves will be presented by Van der Velde et al. (1984). The paper of Brock et al. (1983) deals with the structure, biomass and annual net productivity of the total plant. The objectives of the present paper are:

(1) to describe the seasonal changes in nitrogen and phosphorus content of the various organs of *N. peltata* in the Bemmelse Strang;
(2) to elucidate the distribution of nitrogen and phosphorus in the water, seston, bottom and macrophyte compartments in the stands of *Nymphoides*;
(3) to give an approximation of the annual flux of nitrogen and phosphorus from *Nymphoides* to the detritus compartment;
(4) and to reveal the nitrogen and phosphorus release of decomposing *Nymphoides* leaves.

MATERIALS AND METHODS

Sampling programme and sample preparation

Samples of water were taken biweekly from 7 January until 16 December 1980 from the *N. peltata* stands in the Bemmelse Strang with a Ruttner

water sampler. On each date several subsamples of water (collected from several stands and several depths) were mixed to get one representative water sample. On several days water was also sampled at sites in the Bemmelse Strang without macrophytes (open water) to compare with water from the *N. peltata* stands. Furthermore, on each sampling date the height of the water column, the minimum and maximum temperatures, the pH, and alkalinity of the water from the *N. peltata* stands were measured. Immediately on return to the laboratory a known volume of each water sample was filtered through prewashed glass fibre filters (Whatman GF/C; pore size ca. 1.2 μm). These filters and control blanco filters were dried at 105°C for 24 h and stored. The fraction remaining on the filters is designated as the fine particulate fraction or the seston. The filtered water, representing the dissolved fraction, was stored in 100-ml iodated polyethylene bottles, preserved (0.5 ml 200 ppm $HgCl_2$) and stored (-20°C).

Eleven times from 4 January until 16 December 1980, sediment samples were collected from two stations in the Bemmelse Strang, viz., the *N. peltata* stands and the open water. From each station 10 subsamples of bottom were collected on each date with a brass tube (length 10 cm, diameter 5.6 cm) and thoroughly mixed. The top 10-cm sediment layer was sampled on each date, as it was considered to be the main reservoir of nutrients for the uptake of nitrogen and phosphorus by *N. peltata*. Most roots of *N. peltata* can be found in the top 10 cm (Brock et al., 1983). Since some roots can reach a depth of 30—40 cm, once on 25 October, 5 sediment samples were taken from both stations to a depth of 50 cm with a core device (diameter 8 cm). Each core was immediately separated into 10-cm sections, with the sediment—water interface as a starting point. The corresponding sections of each core were thoroughly mixed.

In the laboratory the specific mass and the water content of each wet, well-mixed, sediment sample were determined. Water soluble sediment nutrients were extracted from 20 g wet sediment by continual agitation for 1 h in 200 ml twice distilled water. The extractions were performed in duplicate for each sediment sample. The extraction water of each sediment sample was then centrifuged (10 min, 500 r.p.m.) to remove sediment particles, stored in 100-ml iodated polyethylene bottles, preserved (0.5 ml 200 ppm $HgCl_2$) and stored (-20°C). The nutrients of the extraction water are considered as belonging to the interstitial water. A part of each wet sediment sample was dried (105°C, 24 h) and stored for further nutrient analysis.

Each month from February until December biomass samples of *N. peltata* were harvested from the Bemmelse Strang along with water and bottom samples (for a detailed description of the harvest methodology and biomass data; see Brock et al., 1983). In the laboratory the *N. peltata* material was cleaned of mud, associated fauna and loose periphyton and divided into roots, short shoots, long shoots, petioles, leaf blades and flowering

structures (flowers, fruits and peduncles). These plant parts were then dried (105°C, 24 h), ground until sample homogeneity was assured visually and stored.

The decomposition experiments were carried out with litter bags according to the method described by Brock et al. (1982). Polyethylene litter bags of 16 × 16 cm were used, with a 0.5-mm mesh size. Green mature *Nymphoides* leaves were cleaned, dried between filter paper, weighed and enclosed in litter bags as undamaged as possible. All litter bag experiments were performed in sets of four. In each litter bag at least ten leaf blades were enclosed in order to obtain a more or less homogeneous sample. Fresh material was used for the decomposition experiments because predrying of plant material affects weight loss and nutrient release during breakdown (Brock et al., 1982; Rogers and Breen, 1982). The initial fresh weight of the material enclosed in each litter bag was printed on a rotex tape, which was placed in the litter bags (in order to know the initial weight of the decomposing tissues). The dry weight and the nitrogen and phosphorus content per g dry weight of the *Nymphoides* material was determined at the beginning of each experiment from replicate samples. Two series of litter bags were incubated in the dark in temperature rooms of 8°C and 20°C, respectively. Each litter bag was placed in a 1-l glass jar, filled with 750 ml Bemmelse Strang water (see Bastardo, 1979). A blank series of glass jars, containing only Bemmelse Strang water, was also placed in each temperature room. After 4, 7, 19, 32 and 46 days, four jars with litter bags as well as four blank jars were retrieved from each temperature room. The coarse particulate plant material was removed from the bags, dried, weighed and stored. Furthermore, on each sampling day a known volume of water from each glass jar was filtered through prewashed glass fibre filters (Whatman GF/C). These filters, with fine particulates, were dried and stored for further analysis. The filtered water was stored in 100-ml iodated polyethylene bottles, preserved (0.5 ml, 200 ppm $HgCl_2$) and stored (20°C). For each sampling day, the measured values of the controls were subtracted from those of the jars with litter bags.

Nutrient analysis

The soluble nitrogen of water and bottom extraction samples was analysed with a Technicon autoanalyser as three components: nitrate and nitrite-nitrogen (Kamphake et al., 1967), ammonia-nitrogen (Grasshoff and Johannsen, 1968) and total nitrogen (Armstrong et al., 1966; Armstrong and Tibbits, 1968). The dissolved organic nitrogen is considered to be the difference between total nitrogen and inorganic nitrogen (nitrate/nitrite and ammonia) (Golterman et al., 1978). The dissolved phosphorus of the water and extraction samples was analysed with a Technicon autoanalyser as two components: orthophosphate or molybdate reactive phosphorus (Hendriksen, 1965) and total phosphorus (Armstrong and Tibbits,

1968; Stanley and Richardson, 1971). The difference between total phosphorus and orthophosphate is considered to be the hydrolysable phosphate, being the phosphorus bound to organic substances and polyphosphate (Golterman et al., 1978). In order to determine the nitrogen and phosphorus content of the particulate fractions, dried samples of carefully weighed particulate material (material on Whatman GF/C filters, plant material and sediment) were digested under pressure in a mixture of concentrated perchloric acid and sulphuric acid in teflon digestion bombs (4 h, 170°C) according to the method described by Kotz et al. (1972). The digestions, followed by nitrogen and phosphorus analysis using a Technicon autoanalyser, were performed in duplicate in the case of seston and macrophyte samples and in triplicate in the case of sediment samples. Furthermore, samples of water, filters with particulates and *Nymphoides* material were analysed for organic carbon with an Oceanography International carbon analyser (model 05224 B-AA), modified according to Roelofs (1983). In our figures and tables the mean values of the different nutrient analysis per sample are presented. No standard deviations are given because due to time limitation we decided to mix all subsamples of each compartment on each sampling day to get one representative sample for nutrient analysis per compartment and per sampling day.

RESULTS AND DISCUSSION

Nitrogen and phosphorus accumulation by N. peltata

We observed that the nitrogen and phosphorus concentrations showed marked differences per plant part and per sampling day (Figs. 1 and 2). The N and P levels in all structures of *N. peltata* peaked during spring, declined to their lower values during summer and then increased again in late summer and autumn. High concentrations of nitrogen and phosphorus before the main growing season may be the result of active nutrient uptake, followed by rapid protein synthesis before the onset of fast growth. The sharp decline in nitrogen and phosphorus concentrations in the underground tissues, accompanied by a rise in N and P levels in above-ground plant parts in the period April—May may partly be due to translocation of these elements to above-ground tissues. The decline of nitrogen and phosphorus concentrations during summer coincides with the period of rapid biomass increase. This may be attributed to a faster utilization than uptake in this period, so that stored nitrogen and phosphorus resources are gradually 'diluted' during growth. The clear rise of nitrogen and phosphorus levels in underground tissues in the period September—October may be caused by reallocation of N and P from above-ground plant parts and/or active uptake from the hydrosoil while growth has stopped.

Generally, the underground structures had higher nitrogen and phos-

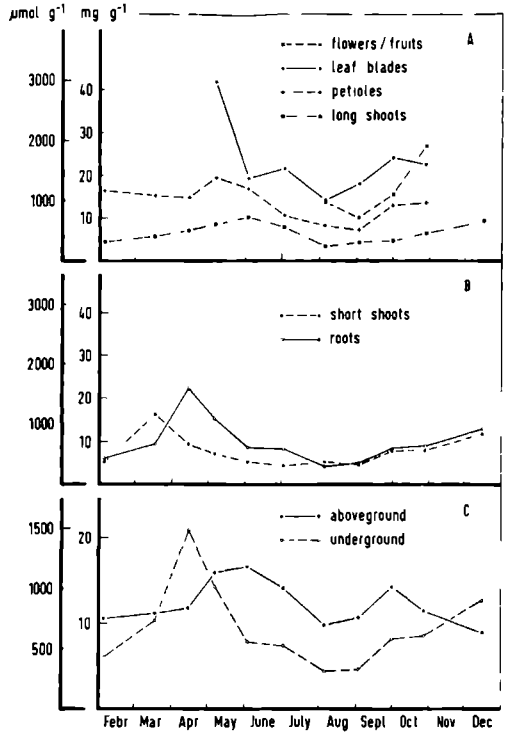

Fig. 1. (A) Seasonal changes in nitrogen content of various above-ground organs of *N. peltata*. (B) Seasonal changes in nitrogen content of various underground organs of *N. peltata*. (C) Seasonal changes in nitrogen content of the above-ground and underground biomass.

phorus concentrations before and after the main growing season, while during summer the above-ground plant parts had higher N and P contents. The leaves, the important sites for photosynthesis, especially had high concentrations in comparison to other plant parts. The nitrogen and phosphorus levels of the leaf blades were higher in July when compared to

TABLE I

The nitrogen and phosphorus concentrations of *N. peltata* leaves of various age in μmol per g dry weight and their atomic N:P ratios. The leaves were sampled on 27 August 1980 in the Bemmelse Strang

	N	P	N:P
Young green leaves	2090	168	12.4
Mature green leaves	1275	93	13.7
Mature yellow leaves	1288	90	14.3
Senescent leaves	1281	74	17.3
Decaying leaves	1363	66	20.7

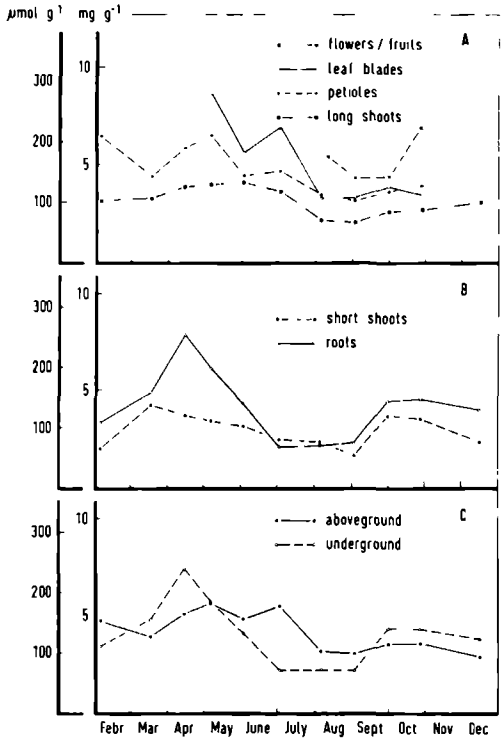

Fig. 2. (A) Seasonal changes in phosphorus content of various above-ground organs of *N. peltata*. (B) Seasonal changes in phosphorus content of various underground organs of *N. peltata*. (C) Seasonal changes in phosphorus content of the above-ground and underground biomass.

the values of June. This can probably be attributed to a sudden increase in water level at the end of June, resulting in the disappearance of many old leaves and the development of numerous new ones later on. As is shown in Table I the nitrogen and phosphorus concentrations of *N. peltata* leaves depend on their age and physiological state. The sharp rise in nitrogen and phosphorus concentrations in the reproductive structures (Figs. 1 and 2) at the end of the growing season can probably be attributed to the high N and P storage in fruits and seeds.

In Table II the atomic N : P ratios of the various plant parts of *N. peltata* at each sampling day are presented. It appears that the different morphological structures of *N. peltata* had different atomic N : P ratios (e.g., leaf blades > petioles > long shoots), indicating that specific organs have the potential to accumulate one of these elements relatively more efficiently. Furthermore, the atomic N : P ratios of the various plant parts showed seasonal changes which differed for each plant part. This may be caused by changes in relative availability of nitrogen and phosphorus in the ambient media and/or changes in physiological state of the plant parts (see Table I).

TABLE II

Seasonal changes in atomic N:P ratios of various parts of *N. peltata*

	4-II	17-III	14-III	6-V	2-VI	2—VII	5-VIII	2-IX	30-IX	28-X	16-XII
Flowers/fruits							5.7	5.1	7.8	8.6	
Leaf blades				10.7	7.5	6.3	9.4	11.9	13.7	14.3	
Petioles	5.8	7.6	5.5	6.6	8.3	4.9	5.2	4.9	7.8	7.5	
Long shoots	3.1	3.8	4.0	4.7	5.4	4.8	3.4	4.5	3.8	5.2	6.7
Short shoots	5.8	8.4	5.5	4.6	3.5	3.8	4.9	6.0	4.6	5.8	10.9
Roots	4.0	4.2	6.3	5.6	4.3	8.6	4.2	4.4	4.1	4.2	7.0
Above-ground	4.9	6.2	5.1	6.2	7.6	5.6	6.8	7.6	8.9	7.0	6.7
Underground	3.9	4.7	6.2	5.5	4.2	7.4	4.4	4.6	4.1	4.3	7.3
Total plant	4.4	5.0	6.0	5.6	5.9	5.9	6.1	6.9	6.1	4.9	7.3

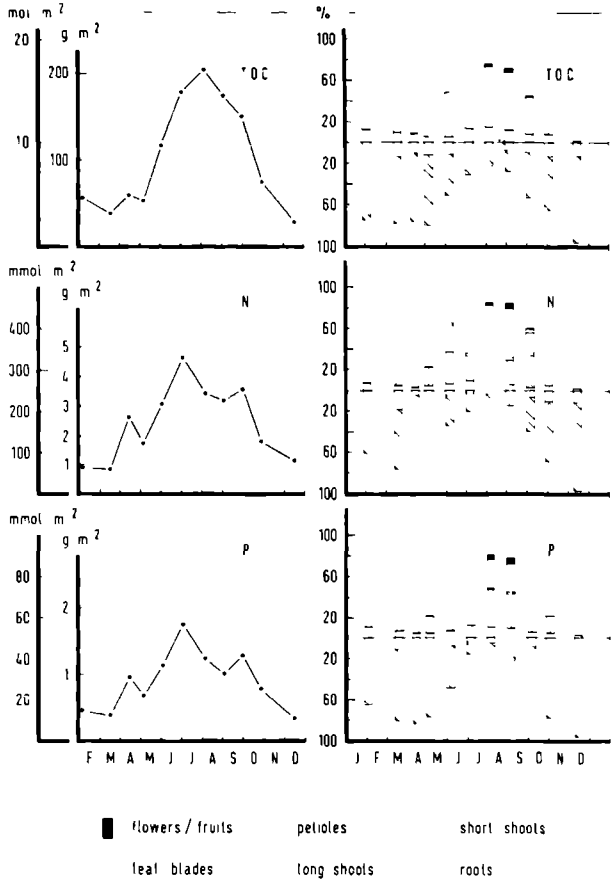

Fig. 3. (Left side) Seasonal changes in organic carbon (TOC), nitrogen (N) and phosphorus (P) stored in *N. peltata* per m^2 of littoral. (Right side) The relative distribution of organic carbon, nitrogen and phosphorus in the various organs of *N. peltata* per m^2 of littoral.

The amount of nitrogen and phosphorus accumulated by *N. peltata* per m^2 sediment surface was calculated for each sampling day by multiplying the concentrations of N and P per g dry weight by the biomass of the various structures per m^2 (given in Brock et al., 1983). In the Bemmelse Strang, *N. peltata* accumulated maximum amounts of nitrogen (334 mmol m^{-2} or 4.7 g m^{-2}) and phosphorus (56.6 mmol m^{-2} or 1.75 g m^{-2}) in July (see Fig. 3 and Tables III and IV). Since the peak organic carbon biomass was reached in August, total nutrient accumulation per m^2 was not simply a function of biomass increase. The graphs of seasonal changes in total nitrogen and total phosphorus stocks per m^2 show the same tendency; these changes in N and P stocks resemble each other more than they do that of TOC per m^2. We also observed that in summer the

TABLE III

Seasonal changes in the nitrogen stocks accumulated by various parts of *N. peltata* in mmol per m^2 of littoral

	4-II	17-III	14-IV	6-V	2-VI	2-VII	5-VIII	2-IX	30-IX	28-X	16-XII
Flowers/fruits							6.86	7.76	0.48		
Leaf blades				0.69	61.21	152.60	113.18	117.54	66.01	0.56	
Petioles	19.55	11.27	19.48	22.84	66.45	79.94	77.06	53.19	78.55	32.07	
Long shoots	4.99	3.20	6.05	5.39	14.40	33.11	14.47	13.98	8.42	6.96	1.83
Short shoots	3.47	11.04	7.79	6.74	9.84	8.63	9.89	7.79	16.38	12.88	9.29
Roots	35.48	35.36	154.64	87.02	64.64	59.50	24.91	26.32	85.97	74.89	69.43
Above-ground	24.54	14.46	25.53	28.91	142.07	265.60	211.57	192.47	153.46	39.59	1.83
Underground	39.01	46.41	162.37	93.76	74.42	68.11	34.81	34.10	102.36	87.77	78.72
Total plant	63.55	60.87	187.91	122.67	216.48	333.71	246.38	226.58	255.82	127.36	80.55

TABLE IV

Seasonal changes in phosphorus stocks accumulated by various parts of *N. peltata* in mmol per m^2 of littoral

	4-II	17-III	14-IV	6-V	2-VI	2-VII	5-VIII	2-IX	30-IX	28-X	16-XII
Flowers/fruits							1.21	1.53	0.06		
Leaf blades				0.06	8.16	24.34	12.08	9.91	4.82	0.04	
Petioles	3.37	1.48	3.51	3.48	7.98	16.20	14.75	10.83	10.07	4.25	
Long shoots	1.62	0.85	1.52	1.14	2.57	6.87	4.30	3.10	2.24	1.33	0.27
Short shoots	0.60	1.32	1.42	1.47	2.79	2.26	2.00	1.29	3.57	2.22	0.85
Roots	8.94	8.49	24.72	15.68	14.98	6.94	5.89	6.04	21.13	17.99	9.90
Above-ground	4.97	2.32	5.03	4.68	18.79	47.41	32.34	25.39	17.20	5.62	0.27
Underground	9.52	9.81	26.14	17.10	17.76	9.20	7.89	7.33	24.70	20.22	10.75
Total plant	14.48	12.13	31.17	21.78	36.56	56.61	40.23	32.71	41.90	25.84	11.02

largest part of the N and P stock can be found above-ground in the laminae and their petioles (Fig. 3).

Nitrogen and phosphorus concentrations in water and sediments

The nitrogen and phosphorus concentrations per litre of overlying water showed considerable fluctuations during the year (Figs. 4A and 5A). The peaks of dissolved nitrogen and phosphorus in late winter are mainly due to nutrient input by the river Waal, which completely flooded the Bemmelse Strang in that period. Flooding of backwaters in winter and early spring is a normal phenomenon in The Netherlands. The smaller peak of dissolved nitrogen in June and the PO_4^{3-} peak in June—July can also be explained by an exceptionally high water level of the river Waal in early summer. In this period the high water level of the Waal did not cause a complete

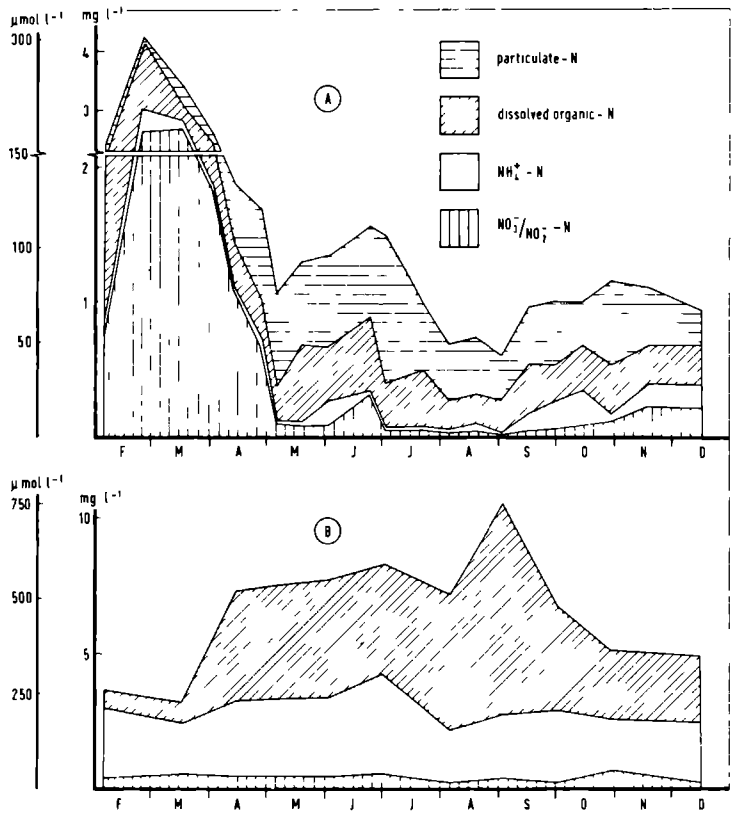

Fig. 4. (A) Seasonal changes in nitrogen content (cumulative) of the overlying water between *Nymphoides*. (B) Seasonal changes in nitrogen concentration (cumulative) of the interstitial water of the *Nymphoides* stands.

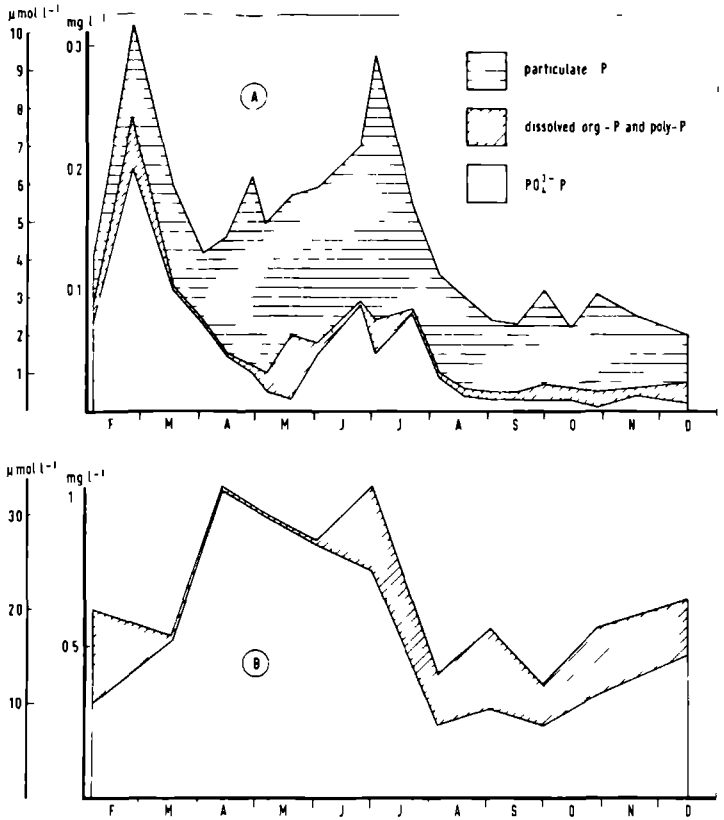

Fig. 5. (A) Seasonal changes in phosphorus concentration (cumulative) of the overlying water between *Nymphoides*. (B) Seasonal changes in phosphorus concentration (cumulative) of the interstitial water of the *Nymphoides* stands.

inundation of the Bemmelse Strang; however, it resulted in the rising of the water level of the former river bed and, consequently, caused input of nitrogen and phosphorus. As a result of the combined effect of high nutrient levels and relatively high water temperatures (Table V) a peak in particulate nitrogen and phosphorus, due to a plankton bloom, was recorded in the beginning of July. The slight increase in dissolved nitrogen in autumn is probably the result of increasing quantities of senescing plants. During the growing season of *Nymphoides* (May—October) the particulate phosphorus fraction of the overlying water was considerably larger than the dissolved phosphorus fraction, while the dissolved and particulate nitrogen fractions were more or less equal. Furthermore, a considerable portion of the dissolved N occurred as dissolved organic nitrogen, while a relatively large part of dissolved P consisted of ortho-phosphate.

The total inorganic nitrogen and inorganic phosphorus contents of the interstitial water were much higher than the concentrations determined

TABLE V

Seasonal changes in chemical and physical conditions of overlying water and bottom between *Nymphoides*

	4-II	17-III	14-IV	6-V	2-VI	2-VII	5-VIII	2-IX	30-IX	28-X	16-XII
Overlying water											
Minimum temperature (°C)	2	3	3	8	11	14	14.5	16	14.5	8	1
Maximum temperature (°C)	2	6.5	11	14	24	24	25.5	22	20	13	12
pH	7.7	8.2	8.3	8.6	8.3	8.5	7.8	8.7	8.7	8.0	7.6
Alkalinity (mEq/l)	—	2.35	2.76	2.62	2.70	2.60	4.57	4.80	—	3.58	1.55
Water depth (m)	1.22	0.91	1.03	0.70	0.84	0.98	1.15	1.05	0.62	0.64	0.57
Bottom											
Redox potential (mV)	−151	−147	−138	−188	−53	−60	—	−341	−272	−183	−318
Specific mass (g/cm^3)	1.16	1.18	1.20	1.16	1.19	1.23	1.19	1.13	1.07	1.09	1.11
% Water	78.5	74.8	71.1	73.3	72.2	67.6	70.0	70.0	70.0	70.0	70.0

in the overlying water (Figs. 4B and 5B). Due to reduced conditions in the sediments (Table V) a large portion of the inorganic N in the interstitial water consisted of NH_4^+. The dissolved phosphorus of the interstitial water consisted mainly of PO_4^{3-}. The P peak of the interstitial water recorded in April—June was probably the result of the sorption of phosphorus to clay particles and the sedimentation of new clay after the flooding by the river Waal.

In Figs. 6 and 7 the nitrogen and phosphorus levels of sediments, interstitial and overlying water of sites with and without *Nymphoides* can be compared. We observed that the nitrogen and phosphorus contents per g dry bottom were largest in the upper 10 cm of the sediment and that the nutrient levels decreased in deeper sections (Figs. 6A and 7A). The

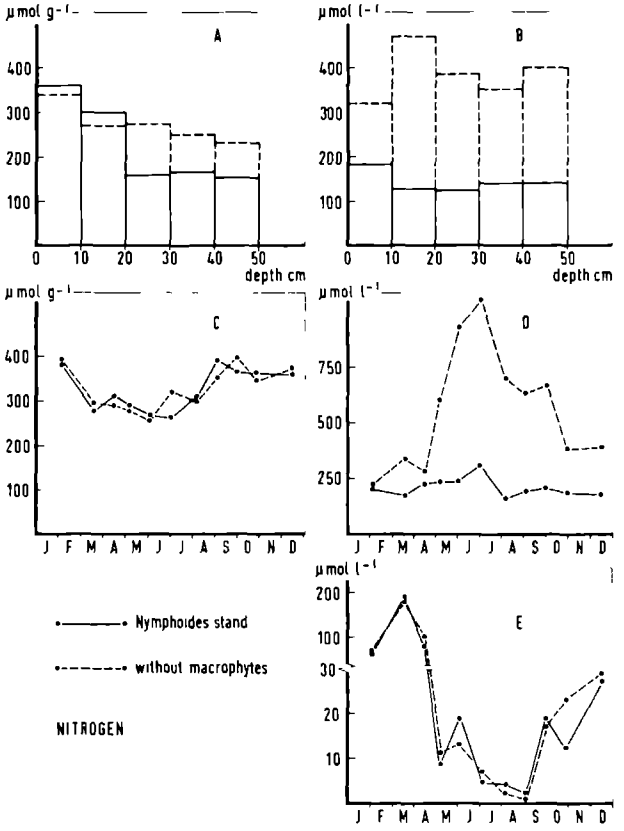

Fig. 6. Comparison between sites with and without *N. peltata*. (A) Nitrogen concentration per g dry weight sediment in a depth profile (10-cm sections). (B) Inorganic nitrogen concentration per l interstitial water in a depth profile (10-cm sections). (C) Seasonal changes in nitrogen concentration per g dry weight bottom of the upper 10-cm sediment layer. (D) Seasonal changes in inorganic nitrogen concentration per l interstitial water of the upper 10-cm sediment layer. (E) Seasonal changes in inorganic nitrogen concentration per l overlying water.

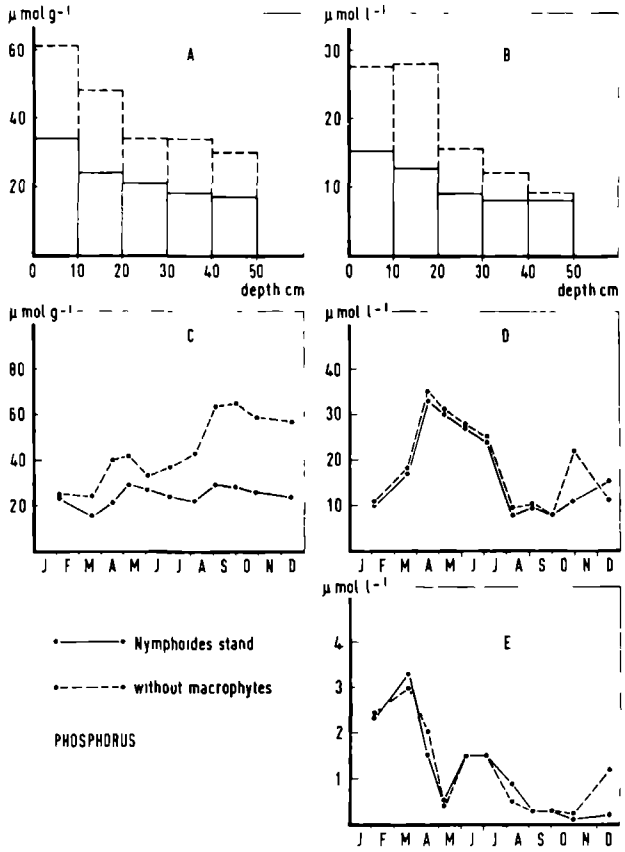

Fig. 7. Comparison between sites with and without *Nymphoides*. (A) Phosphorus concentration per g dry weight sediment in a depth profile (10-cm sections). (B) Inorganic phosphorus concentration per l interstitial water in a depth profile (10-cm sections). (C) Seasonal changes in phosphorus concentration per g dry weight bottom of the upper 10-cm sediment layer. (D) Seasonal changes in inorganic phosphorus concentration per l interstitial water of the upper 10-cm sediment layer. (E) Seasonal changes in inorganic phosphorus concentration per l of overlying water.

sections of the sediment cores (sampled on 25 October) of sites without macrophytes generally showed higher nitrogen and phosphorus concentrations both per g dry weight and per l interstitial water (Figs. 6A, B and 7A, B), with the exception of the N levels per g dry bottom in the upper sections. The high nitrogen and phosphorus concentrations in the upper 10 cm of the sediments are probably due to sedimentation of nutrient rich detritus and possibly also by vertical upward migration of phosphorus (Carignan and Flett, 1981). We observed that the N levels per g dry bottom of the upper 10 cm do not show clear differences between sites with and without *Nymphoides* (Figs. 6C and D). However, the interstitial water of sites without *Nymphoides* showed larger concentrations of inorganic

nitrogen (especially NH_4^+) than that of the *Nymphoides* stands. The inorganic nitrogen levels of the sites without macrophytes were lowest in spring and increased throughout the growing season, presumably due to a greater rate of mineralization and ammonification with increased temperatures. The inorganic nitrogen concentrations of the interstitial water of the *Nymphoides* stands probably remained lower because of nutrient uptake by the macrophyte. We observed that the phosphorus levels per g dry bottom showed clear differences between the two sampling stations (Figs. 7C and D). The phosphorus content per g dry bottom (upper 10 cm) was always higher in the sites without macrophytes. The inorganic phosphorus content of the interstitial water of the two stations was rather similar; however, the hydrosoil of the *Nymphoides* stands mostly showed slightly smaller concentrations. These differences also might be attributed to phosphorus uptake by the macrophyte from the sediments. We noticed that the inorganic nitrogen and phosphorus concentrations per l overlying water did not show clear differences between the two stations (Figs. 6E and 7E). Water from stands with *Nymphoides* probably mixes rather well with water from sites without macrophytes due to the nymphaeid growth form of *Nymphoides* and its occurrence in relatively narrow belts.

Generally it was observed that the sediments and their interstitial water contained higher concentrations of nitrogen and phosphorus than the ambient water and that most nutrients occurred in the upper sediment layers where most roots of *N. peltata* could be found. Nutrient uptake from the sediments by *Nymphoides* is suggested by the larger concentrations of nitrogen and phosphorus in the sediments and/or the interstitial water of the other sample station, devoid of rooted macrophytes.

The distribution of nitrogen and phosphorus in the Nymphoides *stands*

To indicate the quantitative importance of the studied macrophyte with respect to the storage of nitrogen and phosphorus the *N. peltata* dominated system was divided into seston, water, macrophyte and sediment compartments. The seasonal changes in absolute and relative amounts of nitrogen and phosphorus stored in the separate compartments per m^2 of littoral are presented in Tables VI and VII. The nutrient balances presented include the amounts of nitrogen and phosphorus stored in: (1) the whole water column above 1 m^2 at the water—sediment interface; (2) a sediment layer to a depth of 10 cm under this m^2; and (3) the *Nymphoides* biomass per m^2 of littoral. The nutrient concentrations per l (interstitial) water or per g bottom, and the amounts of nitrogen and phosphorus stored in *Nymphoides* per m^2 were presented earlier in this paper. The seasonal changes in water depth of the overlying water and the specific mass and water content of the bottom, necessary for the calculation of total nutrient stores, are reproduced in Table V.

We found that during the whole year most of the nitrogen in the system

TABLE VI

Seasonal changes in the absolute and relative nitrogen stocks present in various compartments of the *Nymphoides* stands in mmol per m^2 of littoral

	4-II	17-III	14-IV	6-V	2-VI	2-VII	5-VIII	2-IX	30-IX	28-X	16-XII
Seston	18.2	24.6	29.7	33.8	41.2	77.6	34.5	23.2	20.6	23.8	10.7
Water	179.3	195.7	108.2	18.9	39.5	27.4	21.9	20.0	19.8	20.5	83.2
Macrophyte	63.6	60.9	187.9	122.7	216.5	333.7	246.4	226.6	255.8	127.4	80.6
Sediment	9602	8266	10804	8915	8865	10600	11140	13390	11825	11968	12121
Total	9863.1	8547.2	11129.8	9090.4	9162.2	11038.7	11442.8	13659.8	12121.2	12139.7	12295.5
Available Inorg. N	94.7	190.4	101.6	26.1	36.5	29.8	17.3	17.5	27.2	20.5	29.0
% Seston	0.18	0.29	0.27	0.37	0.45	0.70	0.30	0.17	0.17	0.20	0.09
% Water	1.82	2.29	0.97	0.21	0.43	0.25	0.19	0.15	0.16	0.17	0.68
% Macrophyte	0.64	0.71	1.69	1.35	2.36	3.02	2.15	1.66	2.11	1.05	0.66
% Sediment	97.35	96.71	97.07	98.07	96.76	96.03	97.35	97.75	97.56	98.59	98.58
% Total	100	100	100	100	100	100	100	100	100	100	100
% Available Inorg. N	0.96	2.23	0.91	0.29	0.40	0.27	0.15	0.13	0.22	0.17	0.24

TABLE VII

Seasonal changes in absolute and relative phosphorus stocks present in various compartments of the *Nymphoides* stands in mmol per m^2 of littoral

	4-II	17-III	14-IV	6-V	2-VI	2-VII	5-VIII	2-IX	30-IX	28-X	16-XII
Seston	1.6	2.5	3.2	2.7	3.4	6.9	3.0	1.4	1.5	1.4	0.7
Water	3.4	3.0	1.6	0.7	1.5	2.4	1.2	0.5	0.4	0.3	0.1
Macrophyte	14.5	12.1	31.2	21.8	36.6	56.6	40.3	32.7	41.9	25.8	11.0
Sediment	561	446	730	891	893	956	788	983	905	850	766
Total	580.5	463.6	766.0	916.2	934.5	1021.9	832.5	1017.6	948.8	877.5	777.8
Available Inorg.-P	3.7	4.5	4.3	3.0	3.6	3.5	1.6	1.0	0.8	1.3	1.3
% Seston	0.28	0.54	0.42	0.30	0.37	0.67	0.36	0.14	0.16	0.16	0.09
% Water	0.59	0.65	0.20	0.08	0.16	0.23	0.14	0.05	0.04	0.03	0.01
% Macrophyte	2.49	2.61	4.07	2.38	3.91	5.54	4.83	3.21	4.42	2.94	1.42
% Sediment	96.64	96.20	95.31	97.25	95.56	93.55	94.67	96.60	95.38	96.87	98.48
% Total	100	100	100	100	100	100	100	100	100	100	100
% Available Inorg.-P	0.64	0.97	0.56	0.33	0.39	0.34	0.19	0.10	0.09	0.15	0.17

(96—99%) could be traced in the sediments (Table VI). The maximum amount of nitrogen accumulated by *Nymphoides* was attained in July, ca. 3% of the nitrogen present in the system. At that time the water and seston compartments only contained 0.25% and 0.79%. During the whole year the inorganic nitrogen (NO_3^-, NO_2^-, NH_4^+) available per m^2 in both the overlying and interstitial water only amounted to 17—190 mmol, while the nitrogen store in *Nymphoides* ranged from 61 to 334 mmol. Although a large portion of the nitrogen in the system was not directly available to the macrophyte, *Nymphoides* apparently used and stored a large amount of the available inorganic nitrogen.

From Table VII it appears that during the sampling period, most of the phosphorus in the system (94—98%) could be found in the bottom compartment. In July, *Nymphoides* stored a maximum of 5.5% of the total phosphorus in the system. The amounts of phosphorus stored in the water and seston compartments were low when compared to that of the macrophyte. Throughout the year, the orthophosphate present per m^2 of littoral in both the overlying and interstitial water only amounted to 0.8—4.5 mmol, while the phosphorus store in *Nymphoides* ranged from 11.0 to 56.6 mmol. Apparently *Nymphoides* accumulated a large amount of the available orthophosphate, although most of the phosphorus in the sediment was not directly available for macrophytic uptake.

It appears that the lowest amounts of nitrogen and phosphorus per m^2 of littoral were found on 17 March, the first sampling day after the flooding of the Bemmelse Strang by the river Waal (Tables VI and VII), although the river caused nutrient input in the water compartment. Apparently the flooding of the Bemmelse Strang by the river Waal also resulted in nutrient loss from the bottom compartment, because of washing away of the nutrient-rich upper sediment layer. Afterwards the nutrient store in the sediment compartment increased again probably due to the settlement of material and/or upward migration of nutrients within the sediment.

Generally, it can be concluded that throughout the year the upper 10 cm of the sediment contained ca. 94—99% of the total nitrogen and phosphorus in the system. The nutrient store of the macrophyte compartment was relatively small when compared with that of the sediment compartment, but relatively large in comparison with those of the water and seston compartments. The upper layers of the sediment are an enormous reservoir of nutrients most of which are not directly available to macrophytes. However, *Nymphoides* apparently accumulates the available inorganic nitrogen and phosphorus efficiently.

Annual nitrogen and phosphorus cycling

Twilley (1976) based an estimation of annual phosphorus cycling by *Nuphar* on the turnover rate of the biomass. This method is applied here

to estimate the annual flux of nitrogen and phosphorus from *Nymphoides* to the detritus compartment. To calculate annual nitrogen and phosphorus cycling the mean nitrogen and phosphorus stocks from the various morphological structures were multiplied by their turnover rates (see Brock et al., 1983). The vegetation period of the above-ground organs was considered to start in May and to end in October. The nitrogen and phosphorus contribution of the flowering structures to the detrital pool is considered to be equal to their maximum N and P stock. The mean nitrogen and phosphorus standing stocks of the other above-ground structures were calculated from data in Tables III and IV for the intervals 6 May—2 June, 2 June—2 July, 2 July—5 August, 5 August—2 September, 2 September—30 September and 30 September—28 October. From these data the annual mean nutrient standing stocks were calculated. The underground structures persisted throughout the whole year so that their annual mean nitrogen and phosphorus stocks could be calculated from results of all sampling days.

It appears that the annual flux of nitrogen from *Nymphoides* to the detritus compartment amounted to ca. 1188 mmol or 16.6 g per m^2 (Table VIII), on average 10.8% of the nitrogen present in the *Nymphoides* dominated system. The annual flux of phosphorus from *Nymphoides* to the detritus compartment was ca. 164 mmol or 5.1 g per m^2, on an average 19.7% of the phosphorus in the whole system (Tables VI and VII). Leaf-blades especially and, to a lesser extent, the petioles contributed to the annual flux of nitrogen and phosphorus to the detritus compartment.

We found that the nutrient release of *Nymphoides* leaves is temperature dependent (Fig. 8). On all sampling days lower amounts of nitrogen and phosphorus were found in the remaining coarse detritus in the 20°C temperature room. At both 8° and 20°C phosphorus disappeared at a

TABLE VIII

The annual mean nutrient stocks of various plant parts of *Nymphoides* and the estimated annual flux of nitrogen and phosphorus from *Nymphoides* structures to the detritus compartment in mmol per m^2 of littoral

	Mean standing stock		Turnover rate	Cycled annually	
	N	P		N	P
Flowers/fruits				7.76	1.53
Leaf blades	85.19	9.89	8.65	736.89	85.55
Petioles	63.77	10.62	5.84	372.42	62.02
Long shoots	15.09	3.39	1.39	20.98	4.71
Short shoots	9.43	1.80	0.67	6.32	1.21
Roots	65.29	12.79	0.67	43.74	8.57
Above-ground				1138.05	153.81
Underground				50.06	9.78
Total plant				1188.11	163.59

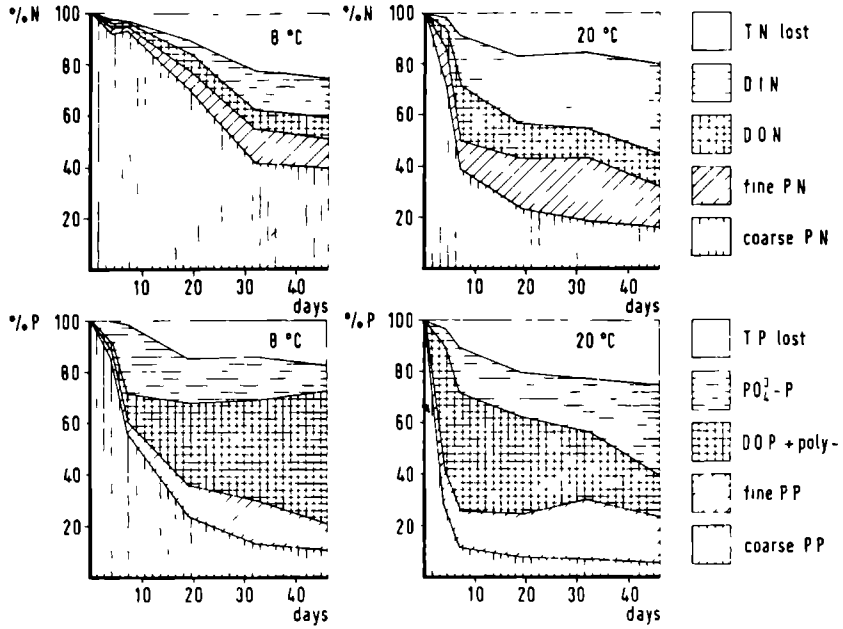

Fig. 8. Nutrient dynamics during breakdown of *N. peltata* leaves, expressed as the percentage of the original stock of each nutrient (in its various forms) remaining in glass jars at each sampling day. TN = total nitrogen; DIN = dissolved inorganic nitrogen; DON = dissolved organic nitrogen; PN = particulate nitrogen; TP = total phosphorus; DOP = dissolved organic phosphorus; PP = particulate phosphorus.

faster rate from the coarse detritus than did nitrogen. During breakdown fine particulate material, dissolved organic matter and inorganic nutrients were released from the coarse detritus. A considerable proportion of the nitrogen and phosphorus could be traced in the fine particulate and dissolved organic fractions. The dissolved organic phosphorus pool especially remained high at 8°C. The decomposing *Nymphoides* material stimulated the development of micro-organisms in the water and attached to substrates (coarse and fine particulate detritus, glass walls, litter bags). Apparently, these micro-organisms are able to take up nitrogen and phosphorus both from the dissolved organic and inorganic pools; the rise in the proportion of organic phosphorus at 8°C after day 19 and the increase of the fine particulate phosphorus pool at 20°C between days 19 and 32 might be explained in this way. The proportions of the various nutrient fractions found in the course of the decomposition experiments are not only dependent on leaching of these fractions from the detritus but also on the metabolism of the organisms present in the jars. In other words, no sooner are the nutrients released, than they are partly trapped again by other components in the system and eventually transformed into other forms. Nevertheless, in most experiments the proportions of inorganic nitrogen and phosphorus in the jars increased with time; this process was

temperature-dependent. In the course of all experiments a considerable proportion of nitrogen and phosphorus could not be detected any more. A certain amount of nitrogen probably disappeared as gaseous decomposition products, but phosphorus could not have disappeared in this way. It was, however, almost impossible to remove all the attached particulates (e.g., micro-organisms) from the glass walls and litter bags in a correct way; a part of the lost nutrient pool was probably stored in these particulates.

Generally, it can be concluded that *N. peltata* has the potential to contribute considerably to the annual flux of nitrogen and phosphorus to the detritus compartment. During breakdown a fast decrease of coarse particulate detritus was accompanied by an increase in fine particulate and dissolved detritus. Furthermore, there was a relatively fast net conversion of organically bound N and P to inorganic forms, especially at higher temperatures.

GENERAL DISCUSSION

Information on the elemental composition of *N. peltata* is scarce. A comparison of our results with those of other studies (see Table IX) shows that in the Bemmelse Strang *N. peltata* had low nitrogen concentrations, fairly normal phosphorus levels and, as a consequence, low atomic N:P ratios. Also when compared with data of other macrophytes, presented by Hutchinson (1975), it appears that *N. peltata* had low atomic N:P ratios. The phosphorus content of *N. peltata* in the Bemmelse Strang was well above the growth-limiting level (1.3 mg g^{-1} or 42 μmol g^{-1}) established experimentally by Gerloff and Krombholz (1966) for several submerged macrophytes. The nitrogen contents of all *Nymphoides* structures, except the leaf blades, were at least periodically below the limiting level (13 mg g^{-1} or 928 μmol g^{-1}) mentioned by these investigators. Different species, however, can have different growth-limiting levels (Gerloff, 1975; Carpenter and Adams, 1977; Barko and Smart, 1979). Species-specific growth-limiting phosphorus and nitrogen concentrations are not known for *N. peltata*. It is difficult to say to what extent the low nitrogen levels and N:P ratios

TABLE IX

Literature data of nitrogen and phosphorus contents of above-ground *Nymphoides peltata* in μmol per g dry weight in July—August

	N	P	N:P
Vavruška (1966) (cited in Dykyjova, 1979)	1999	207	9.7
Riemer and Toth (1968)	1264	136	9.3
This study	695—1023	100—180	5.6–7.6

are due to species-specific or environmental conditions. Concerning the elemental composition of *N. peltata*, the following general remarks can be made:

(1) The different plant parts of *Nymphoides* have different nitrogen and phosphorus levels and N:P ratios (Figs. 1 and 2; Table II). The structural differentiation of the macrophyte is reflected by its chemical composition.

(2) Concentrations of nitrogen and phosphorus and N:P ratios of plant parts are influenced by locality and, thus, by different environmental conditions (Table IX).

(3) The age (physiological state) of a plant part influences its nitrogen and phosphorus content and N:P ratio (Table I).

(4) The nutrient levels and N:P ratios of all plant parts show seasonal changes (Figs. 1 and 2; Table II); this phenomenon can at least partly be explained by changing environmental conditions and by changes in the physiological state of the plants.

(5) The data obtained from regular nitrogen and phosphorus analysis of all plant parts suggest translocation of nutrients. The high underground nutrient levels in winter and spring may be an important characteristic of *Nymphoides*, and other macrophytes because a redistribution of these nutrients may suffice for early growth (see also Bernard and Solsky, 1977).

Macrophytes serve both as a nutrient sink and source; they take up nutrients from the ambient environment for growth and they also supply nutrients to the surroundings by active excretion or decay (Wetzel, 1975). In the Bemmelse Strang the nutrient store in the bottom was enormous in comparison with that of the overlying water and that of *Nymphoides* (Tables VI and VII). Furthermore, nitrogen and phosphorus concentrations were higher in the interstitial water when compared to the overlying water (Figs. 4 and 5). Nutrient uptake from the sediments by *Nymphoides* is suggested by the larger concentrations of nitrogen and phosphorus in the sediments and/or interstitial water of the sample station which was devoid of rooted macrophytes (Figs. 6 and 7). Several studies on rooted aquatic macrophytes demonstrated that the sediments can provide the major source of phosphorus (e.g., Twilley, 1976; Barko and Smart, 1980; Carignan and Kalff, 1980) and nitrogen (Best and Mantai, 1978; Peverly, 1979; Barko and Smart, 1981). Using the model of phosphorus uptake, presented by Carignan (1982), it can be calculated that in the Bemmelse Strang *Nymphoides* absorbed *c.* 80% of its phosphorus needs from the sediments. This is probably an underestimate because this model only accounts for submerged macrophytes, while *Nymphoides* is a floating leaved macrophyte in which upward nutrient translocation is facilitated by evaporation. During the growing season of *Nymphoides* most of the absorbed nitrogen and phosphorus accumulated in the above-ground plant parts (Fig. 3). Furthermore, the above-ground structures contributed most to the annual

flux of nitrogen and phosphorus to the detritus compartment (Table VIII). Thus, there must be an active net translocation of nitrogen and phosphorus from underground to above-ground structures. Decomposing *Nymphoides* leaves appeared to have a rapid nitrogen and phosphorus release, both in the field (Brock et al., 1982) and under laboratory conditions (Fig. 8). For macrophyte nutrient regeneration active excretion, damage caused by animals, autolysis, leaching, microbial breakdown and, according to Miura et al. (1978), browsing by detritivores can be important. Barko and Smart (1980) considered the principal means of nutrient release from macrophytes to be tissue decay. In the Bemmelse Strang, losses of biomass from *N. peltata* were continuous; the above-ground organs especially had high turnover rates. Thus, *Nymphoides* has the potential to regenerate sediment nitrogen and phosphorus during the entire growing season. In spite of the expected flux of nitrogen and phosphorus from decomposing *Nymphoides* to the water compartment, a clear difference in concentrations of these nutrients in the water was not detected between sites with and without *Nymphoides*. We assume that a good exchange of water occurred between sites with and without *Nymphoides*. Enclosures used by Landers (1982) eliminated water exchange between macrophyte beds and open areas. This investigator showed that in enclosures nitrogen and phosphorus levels as well as periphyton and phytoplankton increased in waters surrounding senescing aquatic plants. Sediments can also serve as a net sink for nutrients. Best et al. (1982) showed that during decomposition of *Phragmites*, nutrients became absorbed to the sediments. Of particular importance can be the removal of nutrients from the water column by suspended sediments under aerobic conditions (Holdren and Armstrong, 1980). Sediment traps in the Bemmelse Strang showed that deposition and resuspension of sediment particles is a common phenomenon (Brock, unpublished data). Also the nutrients stored in the more refractory coarse detritus settle and accumulate in the upper sediment layers. Thus, there are several mechanisms that retain and trap nutrients within the community.

It might be argued that our estimate of the annual flux of nitrogen and phosphorus from *Nymphoides* to the detritus compartment is an overestimate. In nature, individual organs mostly die gradually when connected to the plant. If nutrient cycling of macrophytes is estimated by means of the turnover rate of the biomass and if translocation occurs, an overestimate is easily made. The nutrients that are withdrawn from one floating leaf, prior to its senescence, can be used to initiate the growth of another. Resorption of nitrogen and phosphorus from ageing leaves is suggested by the results of the nutrient analysis of the various organs. In the field, however, it is difficult to quantify the effect of resorption of nutrients prior to senescence, e.g., because of differences in decay patterns of the organs. There is a lack of knowledge concerning the internal nutrient recycling mechanism in aquatic vascular plants which certainly needs further attention.

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REFERENCES

Armstrong, F.A., Williams, P.M. and Strickland, J.D., 1966. Photo-oxidation of organic matter in seawater by u.v. radiation. Nature, 211: 481.

Armstrong, F.A. and Tibbits, S., 1968. Photochemical combustion of organic matter in seawater, for nitrogen, phosphorus, and carbon determination. J. Mar. Biol. Assoc., U.K., 48: 143—152.

Barko, J.W. and Smart, R.M., 1979. The nutritional ecology of *Cyperus esculentus*, an emergent aquatic plant, grown on different sediments. Aquat. Bot., 10: 229—238.

Barko, J.W. and Smart, R.M., 1980. Mobilization of sediment phosphorus by submersed freshwater macrophytes. Freshwater Biol., 10: 229—238.

Barko, J.W. and Smart, R.M., 1981. Sediment-based nutrition of submersed macrophytes. Aquat. Bot., 10: 339—352.

Bastardo, H., 1979. Laboratory studies on decomposition of littoral plants. Pol. Arch. Hydrobiol., 26: 267—299.

Bernard, M. and Solsky, B.A., 1977. Nutrient cycling in a *Carex lacustris* wetland. Can. J. Bot., 6: 630—638.

Best, E.P.H., Zippin, M. and Dassen, J.H.A., 1982. Studies on decomposition of *Phragmites australis* leaves under laboratory conditions. Hydrobiol. Bull. (Amsterdam), 16: 21—23.

Best, M.D. and Mantai, K.E., 1978. Growth of *Myriophyllum*: sediment or lake water as the source for nitrogen and phosphorus. Ecology, 59: 1075—1080.

Brock, Th.C.M., Arts, G.H.P., Goossen, I.L.M. and Rutenfrans, A.H.M., 1983. Structure and annual biomass production of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Aquat. Bot., 17: 167—188.

Brock, Th.C.M., Huijbregts, C.A.M., Van de Steeg-Huberts, M.J.H.A. and Vlassak, M.A., 1982. *In situ* studies on the breakdown of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae); some methodological aspects of the litter bag technique. Hydrobiol. Bull. (Amsterdam), 16: 35—49.

Carignan, R., 1982. An empirical model to estimate the relative importance of roots in phosphorus uptake by aquatic macrophytes. Can. J. Fish. Aquat. Sci., 39: 243—247.

Carignan, R. and Flett, R.J., 1981. Postdepositional mobility of phosphorus in lake sediments. Limnol. Oceanogr., 26: 361—366.

Carignan, R. and Kalff, J., 1980. Phosphorus sources for aquatic weeds: water or sediments? Science, 207: 987—989.

Carpenter, S.R., 1980. Enrichment of Lake Wingra, Wisconsin, by submersed macrophyte decay. Ecology, 61: 1145—1155.

Carpenter, S.R. and Adams, M., 1977. The macrophyte tissue nutrient pool of a hardwater eutrophic lake: implications for macrophyte harvesting. Aquat. Bot., 3: 239—255.

Dykyjová, D., 1979. Selective uptake of mineral ions and their concentration factors in aquatic higher plants. Folia Geobot. Phytotaxon., 14: 267—325.

Gerloff, G.C., 1975. Nutritional ecology of nuisance aquatic plants. Natl. Environ. Res. Center, Office for Research and Development, U.S. Environmental Protection Agency, Corvallis, OR, 78 pp.

Gerloff, G.C. and Krombholz, P.H., 1966. Tissue analysis as a measure of nutrient availability for the growth of angiosperm aquatic plants. Limnol. Oceanogr., 11: 529—537.

Golterman, H.L., Clymo, R.S. and Ohnstad, M.A.M., (Editors), 1978. Methods for Physical and Chemical Analysis of Fresh Waters. IBP Handbook No. 8, 2nd edn. Blackwell, Oxford, 213 pp.

Grasshoff, K. and Johannsen, H., 1968. A new sensitive method for determination of ammonia in sea water. Water Res., 2: 516.

Hendriksen, A., 1965. An automated method for determining low level concentrations of phosphate in fresh and saline waters. Analyst, 90: 29—34.

Holdren, G.C. and Armstrong, D.E., 1980. Factors affecting phosphorus release from intact lake sediment cores. Environ. Sci. Technol., 14: 79—87.

Howard-Williams, C. and Allanson, B.R., 1981. Phosphorus cycling in a dense *Potamogeton pectinatus* L. bed. Oecologia (Berl.), 49: 56—66.

Hutchinson, G.E., 1975. A treatise of Limnology. III. Limnological Botany, New York, 660 pp.

Kamphake, L.J., Hannah, S.A. and Cohen, J.M., 1967. Automated analysis for nitrate by hydrazine reduction. Water Res., 1: 206.

Kistritz, R.U., 1978. Recycling of nutrients in an enclosed aquatic community of decomposing macrophytes (*Myriophyllum spicatum*). Oikos, 30: 561—569.

Kotz, L., Kaiser, G., Tschöpel, P. and Tölg, G., 1972. Aufschluss biologischer Matrices für die Bestimmung sehr niedriger Spurenelementgehalte bei begrenzter Einwaage mit Salpetersäure unter Druck in einem Teflongefäss. Z. Anal. Chem., 260: 207—209.

Landers, D.H., 1982. Effects of naturally senescing aquatic macrophytes on nutrient chemistry and chlorophyll-*a* of surrounding waters. Limnol. Oceanogr., 27: 428—439.

Miura, T., Tanimizu, K., Iwasa, Y. and Kawakita, A., 1978. Macroinvertebrates as an important supplier of nitrogenous nutrients in a dense macrophyte zone in Lake Biwa. Verh. Internat. Verein Limnol., 20: 1116—1121.

Nichols, D.S. and Keeney, D.R., 1973. Nitrogen and phosphorus release from decaying water milfoil. Hydrobiologia, 42: 509—525.

Peverley, J.H., 1979. Elemental distribution and macrophyte growth downstream from an organic soil. Aquat. Bot., 7: 319—338.

Riemer, D.N. and Toth, S.J., 1968. A survey of the chemical composition of aquatic plants in New Jersey. New Jersey Agric. Exp. Stn. Bull., 820: 1—14.

Roelofs, J.G.M., 1983. An instrumental method for the estimation of organic carbon in seston, macrophytes and sediments. Aquat. Bot., 16: 391—397.

Rogers, K.H. and Breen, C.M., 1982. Decomposition of *Potamogeton crispus* L.: The effects of drying on the pattern of mass and nutrient loss. Aquat. Bot., 12: 1—12.

Sarvala, J., Kairesalo, T., Koskimies, I., Lehtovaara, A., Ruuhijärvi, J. and Vähä-Pükkiö, I., 1982. Carbon, phosphorus and nitrogen budgets of the littoral *Equisetum* belt in an oligotrophic lake. Hydrobiologia, 86: 41—53.

Stanley, G.H. and Richardson, G.R., 1971. The automation of the single reagent for total phosphorus. In: Advances in Automated Analyses. Technicon International Congress 1970, Vol. II: 305—311.

Twilley, R.R., 1976. Phosphorus cycling in *Nuphar* communities. In: M. M. Brinson and G. J. Davies (Editors). Primary productivity and mineral cycling in aquatic macrophyte communities of the Chowan River, North Carolina. Water Resources Research Institute Publication, University of North Carolina, pp. 36—91.

Van der Velde, G., 1980. Studies in nymphaeid-dominated systems with special emphasis on those dominated by *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Thesis Nijmegen, Stichting Studentenpers Nijmegen, 163 pp.

Van der Velde, G., 1981. A project on Nymphaeid-dominated systems. Hydrobiol. Bull. (Amsterdam), 15: 185--189.

Van der Velde, G., Van der Heijden, L.A., Van Grunsven, P.A.J. and Bexkens, P.M.M., 1984. Development and productivity of the floating leaves of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Aquat. Bot., submitted.

Van Vierssen, W., 1982. The ecology of communities dominated by *Zannichellia* taxa in Western Europe. III. Chemical ecology. Aquat. Bot., 14: 259—294.

Wetzel, R.G., 1975. Limnology. W.B. Saunders, Philadelphia, 743 pp.

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ASPECTS OF THE DECOMPOSITION OF *NYMPHOIDES PELTATA* (GMEL.)O.KUNTZE (MENYANTHACEAE)*

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ABSTRACT

Brock, T C M , 1984 Aspects of the decomposition of *Nymphoides peltata* (Gmel)O Kuntze (Menyanthaceae) *Aquat Bot* , 19 131—156

Aspects of the decomposition of the floating leaved macrophyte *Nymphoides peltata* (Gmel)O Kuntze were studied in the field and under laboratory conditions Most organs of *N peltata* showed different breakdown rates In the field, the breakdown was influenced by seasonal and spatial factors Depending on the exposure time and site of incubation, there were qualitative and quantitative differences in the populations of macro invertebrates which colonized the *N peltata* detritus Only a limited number of taxa dominated the fauna community Nevertheless, the total number of taxa and individuals in and on the detritus was sometimes very high (up to 750 individuals per g detritus)

In the laboratory, ca 5—6% of the organic weight loss of coarse leaf blade detritus was found to be attributable to autolysis and ca 18—23% to physical leaching of organic substances In the initial phase of the decomposition experiment, bacteria were far more important than fungi in the breakdown of coarse leaf detritus Later on, the role of the fungi in the disappearance of the coarse detritus increased Although the fine particulate and dissolved organic matter was at times a considerable fraction of the total organic carbon pool of decomposing leaves, both the coarse detritus and the total organic carbon pool showed a relatively fast and temperature dependent rate of disappearance In the laboratory, the loss rates of the various elements in the coarse detritus showed the following order K> Na> P> Mg> C> N> Ca> Fe

INTRODUCTION

Within the project on the structure and functioning of nymphaeid-dominated systems (cf. Van der Velde, 1980), work has been done on the growth and annual organic matter production of *Nymphoides peltata* (Gmel.)O. Kuntze (Van der Velde et al., 1979, 1984; Brock et al., 1983a). From these studies, it appeared that *N peltata* has the potential for a high annual net productivity, and that the floating leaves particularly contribute to the production. The energy of production may be transferred to higher trophic

*Contribution No 35 of the nymphaeid project

levels either by consumption of living tissue (grazer food-chain) or by microbial decay followed by browsing by detritivores (detritus food-chain). According to Van der Velde et al. (1982), only a relatively small proportion of the production of *N. peltata* is consumed by herbivores, so most of the material enters the detritus pool. Therefore, knowledge of the decomposition of *Nymphoides* detritus is essential for an understanding of the ecological significance of this macrophyte in the systems studied.

Decomposition is a very complex process, which includes not only the changes in, and loss of, organic matter caused by senescence and breakdown, but also interactions between detritus and decomposers. Macrophyte detritus is subject to physical breakdown, e.g. leaching and fragmentation due to water movements and browsing by animals, and to biochemical breakdown, e.g. autolysis and the action of microbial enzymes. Processes associated with physical and biochemical breakdown interact, and partly occur simultaneously. Micro-organisms, especially fungi and bacteria, are generally regarded as the most important decomposers. Fungi and bacteria produce extra-cellular enzymes, which degrade macromolecules into smaller units; these low molecular weight units are then mineralized by micro-organisms or leach out. In addition, colonizing micro-organisms increase the nutritional value of the detritus and condition it for macro-invertebrate feeding (see e.g., Bärlocher and Kendrick, 1975; Fenchel and Jørgensen, 1977; Federle and Vestal, 1980; Rice and Tenore, 1981).

The most frequently studied aspect of the decomposition of macrophytes is the disappearance of coarse detritus (the breakdown). Under field conditions, weight loss, nutrient release, and colonization of coarse macrophyte detritus by macro-invertebrates are mostly studied by the litter bag (mesh bag) technique. It is assumed that changes in weight, chemical composition and associated microbes and fauna of detritus are similar inside and outside the bags. In other words, that in litter bags the detritus is not isolated from the various environmental factors which determine decomposition in a certain system.

Breakdown rates of senescent aquatic plants are controlled by season-related factors, including the physiological and biochemical state of the plant material, physico-chemical conditions of the environment, and numbers and activities of decomposers. Therefore, a single litter-bag experiment may not be enough to describe the breakdown of macrophyte detritus in a system.

Despite the fact that litter bags are the most simple and widely used technique (which makes comparisons easy), several disadvantages should be mentioned.

(a) The fate of the fine particulate and dissolved organic matter is not studied.
(b) Detritus in litter bags can be subject to contamination by sediment particles and organic matter which is not incubated but is (for example) transported into the bags by invading organisms.
(c) Possible modifications of the micro-environment within the bags may

affect the decomposition of enclosed detritus, e.g. anaerobic conditions due to tightly packed detritus in the bags.

(d) The litter bags themselves serve as a substrate for colonization by macro-invertebrates.

(e) Litter-bag experiments only give an overall picture of various decomposition processes such as autolysis, leaching, microbial action, fragmentation, browsing by detritivores and transport of fine-POM and DOM out of the bags, so that the relative contribution of the different processes in the breakdown of macrophyte detritus cannot be studied in this way.

These disadvantages can be partly overcome by a carefully chosen litter-bag methodology (cf. Brock et al., 1982) and/or by laboratory decomposition studies in which the natural environment is more or less simulated. Laboratory studies, however, have their limitations in being simplified compared to the field situation. Nevertheless, in combination with the in situ decomposition studies, they can be very instructive with respect to the mechanisms underlying decomposition processes.

In the present paper, in situ and in vitro studies on decomposition of *Nymphoides peltata* are presented, which aim at a description of the breakdown of this species in the Bemmelse Strang, an alkaline, eutrophic former bed (or oxbow lake) of the river Waal (The Netherlands). A description of the topographical features of the Bemmelse Strang has been given by Van der Velde et al. (1979), and its chemistry is described by Brock et al. (1983b) and Brock (1983). Special attention is paid to the decomposition of the floating leaves, since these organs, in particular, contribute to the production. More specific objectives of the present paper are:

(1) to report breakdown-rates of the coarse detritus of *Nymphoides peltata*;

(2) to compare the nutrient release of coarse *Nymphoides* detritus under field and laboratory conditions;

(3) to compare the disappearance of the coarse particulate organic matter with that of the total organic carbon pool of decomposing *Nymphoides* leaves;

(4) to elucidate the relative contribution of physical leaching, autolysis, bacteria and fungi during breakdown of *Nymphoides* leaves;

(5) to describe the colonization of the coarse *Nymphoides* detritus by macro-invertebrates.

MATERIALS AND METHODS

General research programme

The *Nymphoides* material used in all decomposition experiments was harvested in the Bemmelse Strang and some neighbouring pools. The field experiments were performed in the Bemmelse Strang in 1980 and 1981. In both the in situ and in vitro experiments, polyethylene litter bags (16 × 16 cm) with a 0.5-mm mesh size were used. The material retained by these litter

bags is indicated in the present paper as the coarse detritus or coarse particulate organic matter. All litter-bag experiments were performed in sets of four. Green, mature *Nymphoides* plant parts were cleaned, placed between filter paper to remove adherent water, weighed and enclosed in litter bags. In all experiments, portions of 20—30 g fresh weight were enclosed in the litter bags (cf. Brock et al., 1982). At least 10 specimens of a specific plant part were enclosed in each litter bag in order to obtain comparable samples. Fresh material was used in the decomposition experiments because predrying of plant material affects weight loss and nutrient release (Brock et al., 1982; Rogers and Breen, 1982). The initial fresh weight of the material enclosed in each litter bag was printed on a rotex tape which was placed in the litter bag. The dry weight and ash content (and in some experiments the elemental composition) of the *Nymphoides* material was determined at the beginning of each experiment from replicate samples. Weight loss of *Nymphoides* structures decomposing in litter bags, was determined at regular intervals during 3—46-day periods. At the end of a certain decay period, the contents of the bags were transferred (quantitatively) to aluminum foil and the dry mass (24 h, 105°C) was determined. Before drying the remaining plant material of the in situ experiments, macro-invertebrates were separated from the detritus and preserved in alcohol (70%). The dried coarse detritus was ground until visual sample homogeneity was obtained. Subsamples were ashed (4 h, 550°C) in a muffle furnace to determine the ash-free dry weight (AFDW). Mean values of remaining organic weight and standard deviations were calculated for the various experiments on each sampling day. These data were compared statistically by using the one way analysis of variance and Scheffé's simultaneous test (Scheffé, 1959).

Mean values of remaining organic weight of most decomposition experiments were fitted into an exponential function of the type $W_t = W_o \cdot e^{-kt}$ (cf. Olson, 1963); W_t is the mass remaining after a time-interval t (in days), W_o is the initial mass and k is the rate constant. This model was used because it is the model most widely used in the literature to describe breakdown of aquatic macrophytes. Furthermore, this model is very convenient for comparative purposes because it only has one rate constant. Breakdown rates were statistically compared by means of the Student t-test.

In some experiments, subsamples of remaining detritus were analysed for organic carbon with an Oceanography International Carbon Analyser, according to the methods described by Roelofs (1983). In order to determine the nutrient content of the coarse detritus, subsamples of dried detritus were digested under pressure in a mixture of concentrated perchloric acid and sulphuric acid in teflon digestion bombs (4 h, 170°C) (cf. Kotz et al., 1972). The digestions, followed by nutrient analyses, as well as the organic carbon analyses, were performed in duplicate. Nitrogen and phosphorus were determined colorimetrically with a Technicon II Autoanalyser. Potassium and sodium were analysed with a Technicon Flame Photometer IV, and magnesium, calcium, iron and manganese with a Beckman Absorption Spectrophotometer.

Breakdown of the different organs

Two in situ experiments and one in vitro experiment were carried out to study the breakdown of the different organs of *Nymphoides peltata*. The in situ experiments (started on 17 July 1980 and 28 August 1981) were designed to simulate the natural circumstances to which the decomposing *Nymphoides* detritus is exposed. Therefore, litter bags with leaf-blades and petioles were allowed to float at the water surface in the *Nymphoides* stands until they became water-logged and sank to the bottom. The bags with the long shoots were anchored to the bottom, while the bags with the short shoots and the roots were buried in the upper layers of the sediment in the *Nymphoides* beds. The corresponding in vitro experiment (started on 9 July 1981) was designed to study the breakdown of the coarse detritus of the various organs of *N. peltata* under defined environmental conditions. Therefore, each litter bag was placed in a jar (diameter 8 cm), containing 750 ml non-sterile water from the Bemmelse Strang; the jars were then incubated in the dark in a temperature-room at 15 ± 1°C. The water in the jars was not aerated, but free diffusion of gases between air and water was allowed. The plant material was incubated in the dark because dark conditions accelerate senescence in green plant parts (cf. Thimann, 1978). Furthermore, algal growth and photosynthetic production is prevented in this way. The methodology used was more or less the same as that of Bastardo (1979).

Decomposition of leaf-blades and colonization by macro-invertebrates

To study the influence of spatial factors on the breakdown and colonization by macro-invertebrates of *Nymphoides* detritus, an experiment was started on 5 June 1981. Three series of litter bags, which contained leaf-blades of *N. peltata*, were incubated along a depth gradient, viz.:

- Series 1, on sites in the littoral helophyte vegetation (dominated by *Glyceria maxima* (Hartm.)Holmb. and *Carex acuta* L.) with a water-depth of 20 ± 10 cm;
- Series 2, on sites in *Nymphoides peltata* beds with a water-depth of 90 ± 10 cm;
- Series 3, on sites with a water-depth of 240 ± 10 cm where no macrophytes occur (the open water).

To assess the effect of seasonal factors on the breakdown of *Nymphoides* detritus, litter bags with leaf-blades were incubated in the *Nymphoides* beds of the Bemmelse Strang on 17 July 1980, 10 October 1980, 5 June 1981, 17 June 1981 and 28 August 1981.

Together with the in situ experiment started on 10 October 1980, a laboratory experiment was carried out. The aims of this laboratory experiment were three-fold, viz.:

(1) to compare organic weight loss and nutrient release of coarse *Nymphoides* detritus under field and laboratory conditions;

(2) to assess the effect of temperature on the organic weight loss and nutrient release of *Nymphoides* detritus;
(3) to study the kinetics of the total organic carbon pool of decomposing *Nymphoides* leaves.

Two series of litter bags with leaf-blades were incubated in the dark (for the reasons mentioned above) in temperature-rooms at 8 ± 1°C and at 20 ± 1°C. Each litter bag was placed in a jar (diameter 8 cm), filled with 750 ml non-sterile Bemmelse Strang water. Control series of jars, containing Bemmelse Strang water only, were also placed in the temperature-rooms. After 4, 7, 19, 32 and 46 days, four jars with and four jars without litter bags were retrieved from both temperature-rooms. A subsample of water from each jar was filtered over a Whatman GF/C filter to determine the amount of fine particulate organic matter present. The amount of organic carbon in the coarse detritus (>0.5 mm), fine particulate detritus (>1.2 μm) and dissolved detritus (<1.2 μm) was analysed; the values found for the controls were subtracted from those for the jars with litter bags.

The relative contributions of different breakdown processes

A laboratory experiment, started on 25 September 1981, was designed to study the relative importance of physical leaching, autolysis, bacteria and fungi in organic weight loss during breakdown of coarse *Nymphoides* detritus. Portions of fresh leaf-blades were enclosed in 80 litter bags; 16 litter bags were placed in an oven for 24 h at 105°C to dry the leaves. Then each litter bag was placed in a jar (diameter 8 cm) containing 500 ml non-sterile Bemmelse Strang water. The antifungal agents nystatin (36 mg l^{-1}) and actidione (50 mg l^{-1}) and/or the antibacterial agents benzylpenicillin (25 mg l^{-1}) and streptomycin (25 mg l^{-1}) were added to the Bemmelse Strang water of some of the jars (the numbers in parentheses represent the concentrations in the jars). Thus, the following combination of treatments were used:
— Treatment 1, pre-dried leaves and water with antibacterial and antifungal agents;
— Treatment 2, fresh leaves and water with antibacterial and antifungal agents;
— Treatment 3, fresh leaves and water with antibacterial agents;
— Treatment 4, fresh leaves and water with antifungal agents;
— Treatment 5, fresh leaves and water without antibiotics (control).

It is assumed that by drying the *Nymphoides* leaves, the macrophyte's enzymes become inactivated so that autolysis (the breakdown of organic matter due to the plant's enzymes during senescence) does not take place. It is therefore also assumed that the weight loss (at least in the initial phase) of the leaves in Treatment 1 is due to physical leaching of water-soluble components only. The antibiotic doses used were more or less identical to those applied by Kaushik and Hynes (1971) and Mason (1976). Furthermore, Mason (1976) showed that the antibiotics used are very successful in reducing bacterial and fungal populations, respectively, by over 90%. This experi-

ment was carried out in the dark (for the reasons mentioned above) in a 15 ± 1°C temperature-room. Twice each week, the Bemmelse Strang water with the above-mentioned antibiotic dose was refreshed because the antibiotics used disintegrate slowly at 15°C. Four litter bags from each treatment were removed after 4, 7, 19 and 32 days and processed as described above.

RESULTS

The breakdown of the different organs

In both the field and laboratory experiments, the breakdown of coarse detritus of all organs was rapid, only a small proportion of the initially incubated mass remained after 40 days (Fig. 1). A comparison of the in situ experiments shows differences, particularly in the decay patterns of long shoots, short shoots and roots. These differences cannot be explained by differences in temperature regime (Fig. 1). It seems likely that the chemical composition and physiological state of the plant material at the time of incubation influenced its further fate. In this respect, it is important to know that in the Bemmelse Strang, the leaf-blades and petioles only persisted for a relatively short period in a living state (ca. 23 and 29 days, respectively), while the mean life span of the other organs was much longer. So natural senescence of leaf-blades and petioles was a common phenomenon during the whole growing season, while the long shoots, short shoots and roots generally showed natural senescence at the end of the season only (Brock et al., 1983a). It can be argued that the in situ experiment in July was started too early in the growing season to simulate natural senescence of roots and shoots in a correct way. At the time of harvesting, these organs were "physiologically" young, which might also explain the initial growth of long shoots in the early field experiment; the long shoots are important for the vegetative propagation of *N. peltata*. Therefore, only the breakdown rates of the in situ experiment started on 28 August were calculated.

When the breakdown rates of the different plant parts are compared, it appears that different organs can have different breakdown rates (Table I). In the in situ experiment (started on 28 August), the breakdown rate of the leaf-blades and roots differed significantly from that of petioles, long shoots and short shoots, while that of the short shoots differed significantly from that of long shoots and petioles ($P<0.05$). In the laboratory experiment, also, the breakdown rate of the leaf-blades differed significantly from that of petioles, long shoots and short shoots, while that of the roots differed significantly only from that of short shoots and long shoots, and that of the short shoots from that of the petioles ($P<0.05$). Although the breakdown rate of an aboveground plant part was higher when the initial C/N ratio was smaller, a clear correlation between initial C/N ratio and breakdown rate could not be found when all organs were taken into account (Table I). The largest differences in breakdown rate were found in the in situ

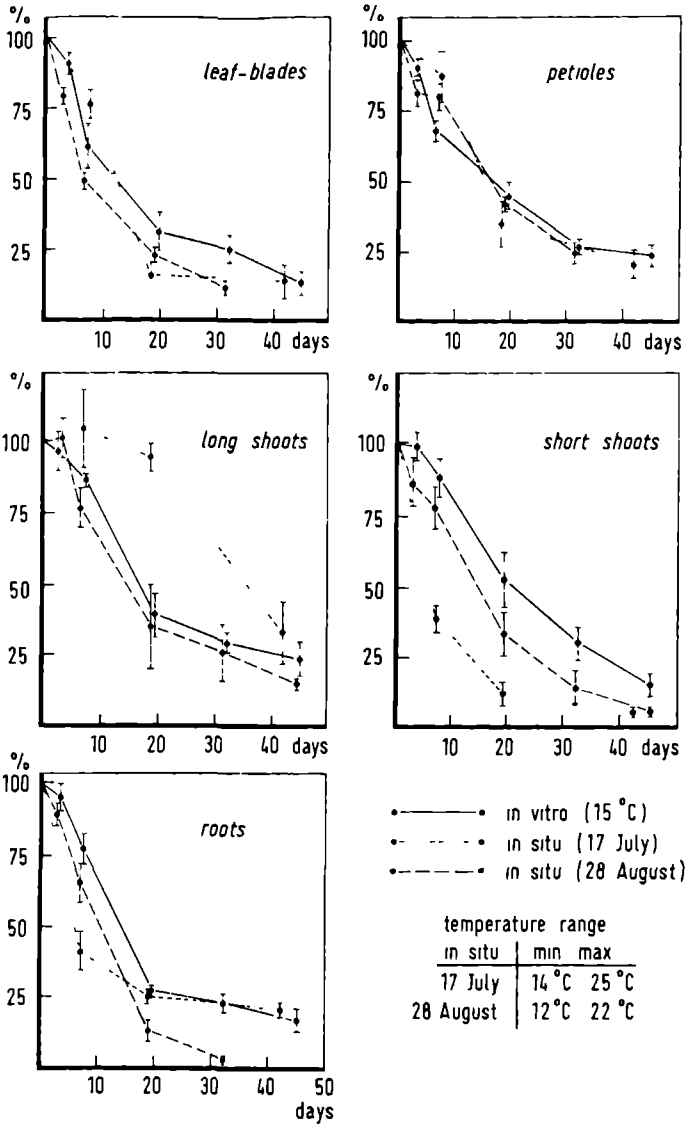

Fig. 1. Mean relative amounts of residual ash-free dry weight and standard deviations of decomposing structures of *Nymphoides peltata* in litter bags.

experiment, a fact which can be explained by the incubation methodology. In the in situ experiment, leaf-blades and petioles were incubated in the overlying water, long shoots on the sediment surface, and short shoots and roots in the sediment of the Bemmelse Strang; in the laboratory experiment, all plant parts decomposed in water. The breakdown rate of leaf-blades, short shoots and roots was significantly higher in the field than in the laboratory (Table I), which can be partly explained

TABLE I

Initial atomic C/N ratios, breakdown rates (k) and corresponding standard errors (se), and coefficients of determination (CD) of *Nymphoides peltata* plant parts

	C/N	k	se	CD
In situ				
Leaf blades	16	0.091	0.007	0.986
Petioles	48	0.045	0.004	0.976
Long shoots	178	0.044	0.005	0.960
Short shoots	152	0.055	0.004	0.986
Roots	179	0.079	0.011	0.964
In vitro				
Leaf blades	22	0.056	0.005	0.974
Petioles	77	0.042	0.003	0.976
Long shoots	151	0.037	0.004	0.954
Short shoots	143	0.035	0.003	0.968
Roots	137	0.049	0.005	0.958

by temperature effects and other environmental conditions associated with the location within the water-sediment column. In addition, the conditions of the in vitro experiment may have allowed the build-up of large concentrations of metabolic products which may inhibit decomposition.

Organic weight loss of decomposing leaf-blades

It was found that the breakdown of coarse leaf-blade detritus in the Bemmelse Strang was influenced by seasonal (Fig. 2A) and spatial (Fig. 2C) factors. The breakdown rate of leaf-blades incubated in the open water differed significantly from that of leaf-blades incubated between *Nymphoides peltata* and littoral helophytes ($P<0.05$) (Table II).

The laboratory experiment showed that the seasonal differences in breakdown of leaf-blades can be largely explained from temperature differences (Fig. 2B). The in vitro experiment, however, showed a higher proportion of residual mass on the last sampling day than the field experiment (Fig. 2A, B). This phenomenon was probably caused by the exclusion of fauna and water movements and by the accumulation of high concentrations of metabolic products, which may have inhibited breakdown in the laboratory experiment.

Figure 3 shows that the decomposition of the total organic carbon pool of *N. peltata* detritus is temperature-dependent. On all sampling days, lower amounts of residual coarse particulate and total organic carbon were found at 20 than at 8°C. During decomposition, fine particulate material and dissolved detritus were transported from the bags to the ambient water. The fine particulate carbon pool was especially high at 20°C, while in the final period of the experiment, the dissolved organic carbon pool was higher at

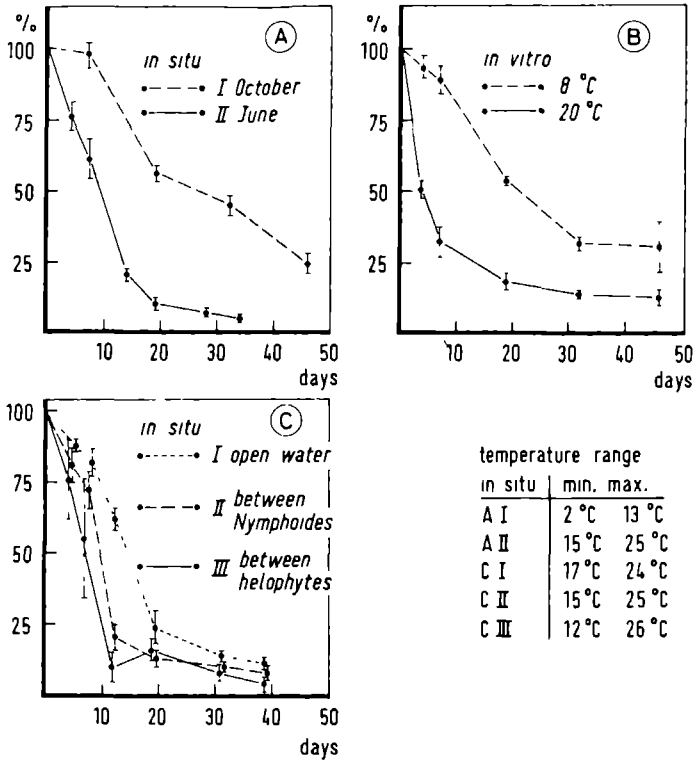

Fig. 2. Mean relative amounts of residual ash-free dry weight and standard deviations of decomposing leaf-blades of *Nymphoides peltata* in litter bags. A, slowest and fastest weight loss observed in the field; B, influence of temperature as observed in the laboratory; C, influence of incubation site in the field.

TABLE II

Breakdown rates (k) and corresponding standard errors (se), and coefficients of determination (CD) of coarse particulate organic matter (cPOM) or total organic matter (TOM) of decomposing leaf-blades of *Nymphoides peltata* (see also Fig. 2)

	k	se	CD
A. In situ (autumn); cPOM	0.027	0.003	0.941
A. In situ (summer); cPOM	0.093	0.009	0.974
B. In vitro (8°C); cPOM	0.030	0.003	0.968
In vitro (8°C); TOM	0.017	0.002	0.954
B. In vitro (20°C); cPOM	0.154	0.027	0.916
In vitro (20°C); TOM	0.037	0.005	0.891
C. In situ (between helophytes); cPOM	0.105	0.015	0.941
C. In situ (between *Nymphoides*); cPOM	0.083	0.013	0.920
C. In situ (open water); cPOM	0.053	0.007	0.941

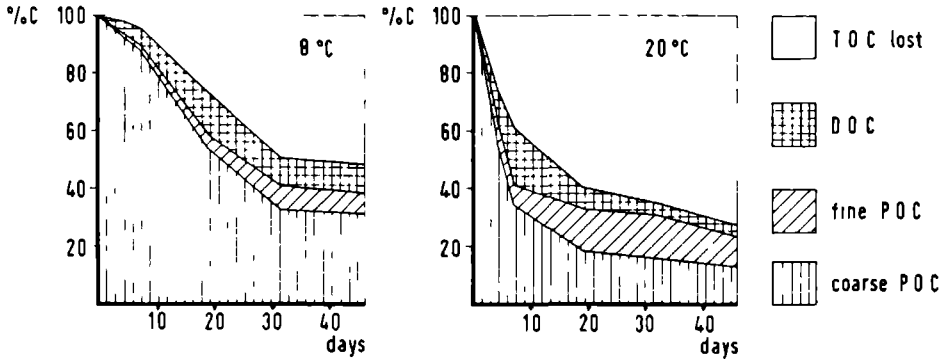

Fig. 3. Organic carbon dynamics during breakdown of leaf-blades of *Nymphoides peltata*. TOC, total organic carbon, DOC, dissolved organic carbon, POC, particulate organic carbon.

8°C. In the course of the experiment, a considerable portion of the organic mass initially incubated apparently disappeared as gaseous decomposition products (e.g. CO_2, CH_4). The decay coefficients of the coarse particulate detritus and the total organic carbon pool were significantly different per experiment and between experiments (Table II).

The relative contributions of different decay processes

The results of the experiments in which leaf-blades of *N. peltata* and antibiotics were used are shown in Fig. 4. The decay patterns of the control

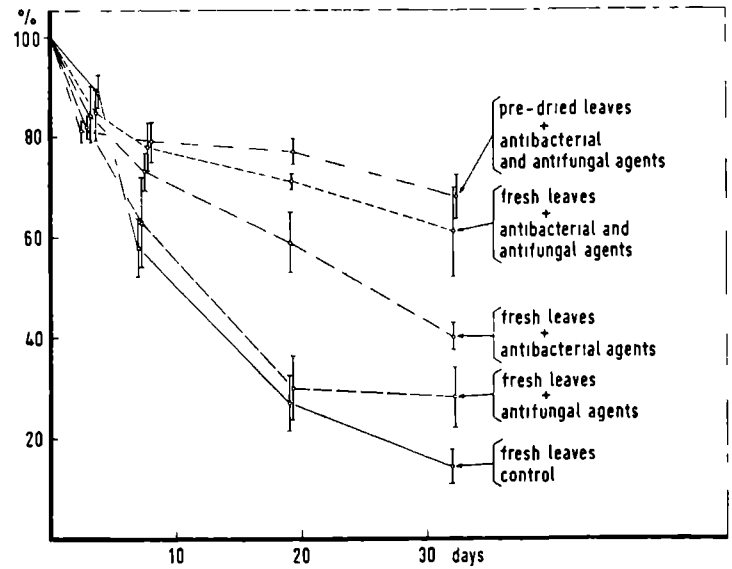

Fig. 4. Mean relative amounts of residual ash-free dry weight and standard deviations of decomposing leaf-blades of *Nymphoides peltata* in litter bags, effects of antibacterial and antifungal agents.

series and the series in which antifungal agents were applied were very similar until sampling Day 19. Apparently, during the initial period (Days 0—19), bacteria were far more important than fungi in the breakdown of *Nymphoides* detritus. Between Days 19 and 32, the residual mass of the control series and the series in which antibacterial agents were used decreased significantly, while that of the series with antifungal agents remained at the same level. This indicates that in the final period of the experiment, the fungi played a greater role in the disappearance of the coarse *Nymphoides* detritus. The control series was found to have a larger residual mass than could be expected from the results of the series in which antibacterial and antifungal agents were used singly. According to Mason (1976), an antagonism may exist between bacteria and fungi; when one group is selectively inactivated the metabolic activity of the remaining group may increase.

The weight loss of coarse detritus in the series in which pre-dried leaves as well as antibiotic agents were used must be attributed to physical leaching, at least in the initial period, amounting to ca. 18—23% of the organic mass initially incubated. Later on, organisms which were not inhibited by the antibiotics used may also have played a (minor) role. The combined effects of antibacterial and antifungal agents resulted in a larger weight loss in the case of the freshly incubated leaves when compared with the series in which pre-dried leaves were used. This difference can probably be explained by autolysis, the disappearance of organic matter due to the action of the plant's enzymes during its senescence, amounting to ca. 5—6% of the organic mass initially incubated.

The nutrient content of N. peltata *detritus*

The nutrient concentration of decomposing leaf-blades and the relative stocks of nutrients remaining in the litter bags for both the field and laboratory experiments are presented in Fig. 5.

In the laboratory, the organic carbon concentration of the coarse detritus slightly increased with time, while that in the field showed a distinct decrease at the end of the experiment. This decrease can be attributed to contamination of the detritus by, e.g., sediment particles. The relative stock of organic carbon remaining in the litter bags decreased steadily with time. This decrease was temperature-dependent. The breakdown patterns of the leaves in the field experiment (in autumn) and that of the leaves in the 8°C laboratory experiment were very similar.

The nitrogen concentration of the detritus showed a clear increase in the first part of the experiment and a slight decrease later on. This decrease was more pronounced in the field experiment, which can probably also be attributed to contamination of the detritus by sediment particles. The relative stock of nitrogen remaining in the litter bags decreased with time, and this decrease was again temperature-dependent.

In both the field and laboratory experiments, the phosphorus, potassium

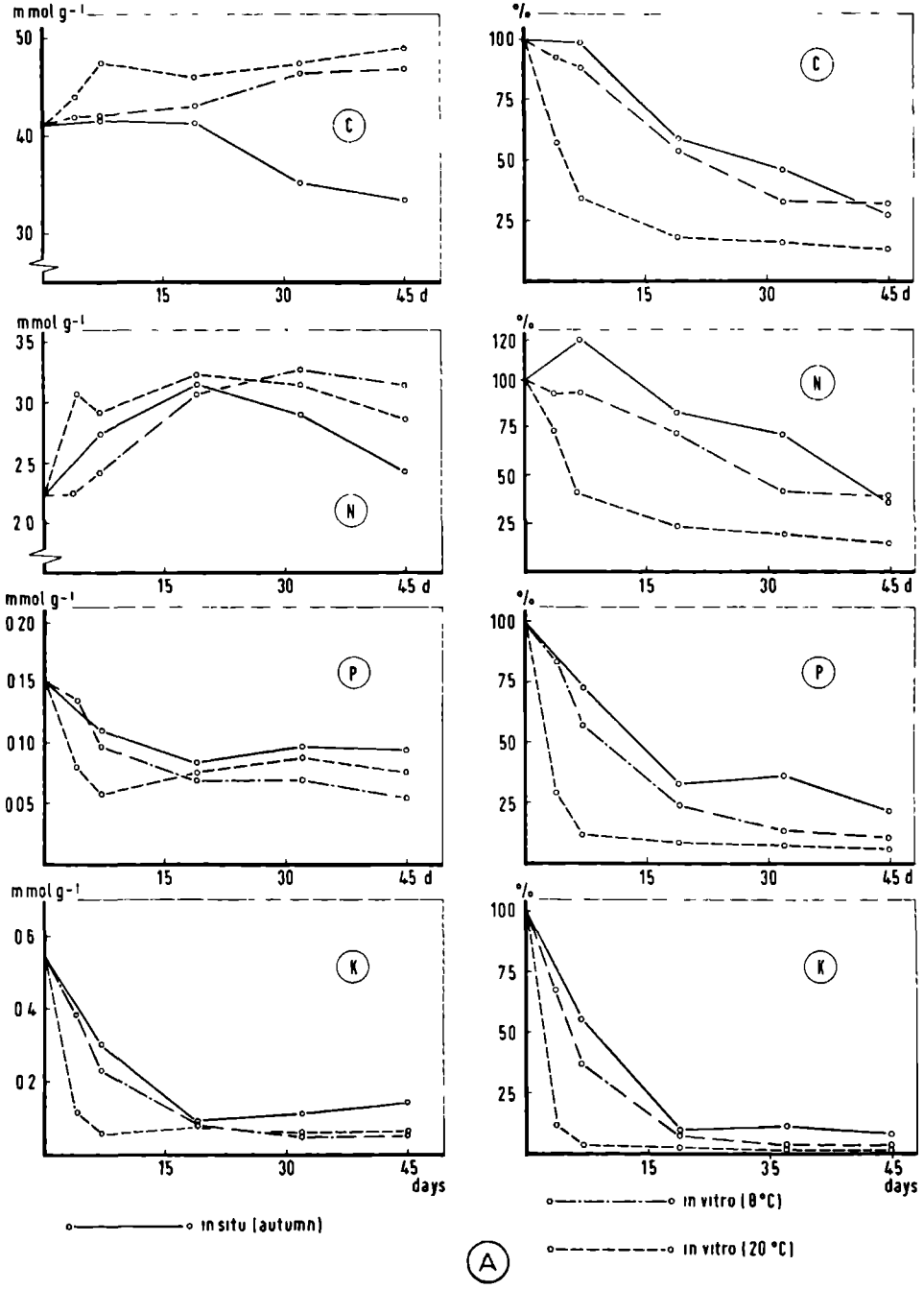

Fig. 5. A. Carbon, nitrogen, phosphorus and potassium dynamics during breakdown of *Nymphoides peltata* leaf-blades in the field (solid line) and the laboratory (dotted lines), expressed as mmol per g dry weight (left) and as percentage of the original stock (right) remaining in the litter bags.

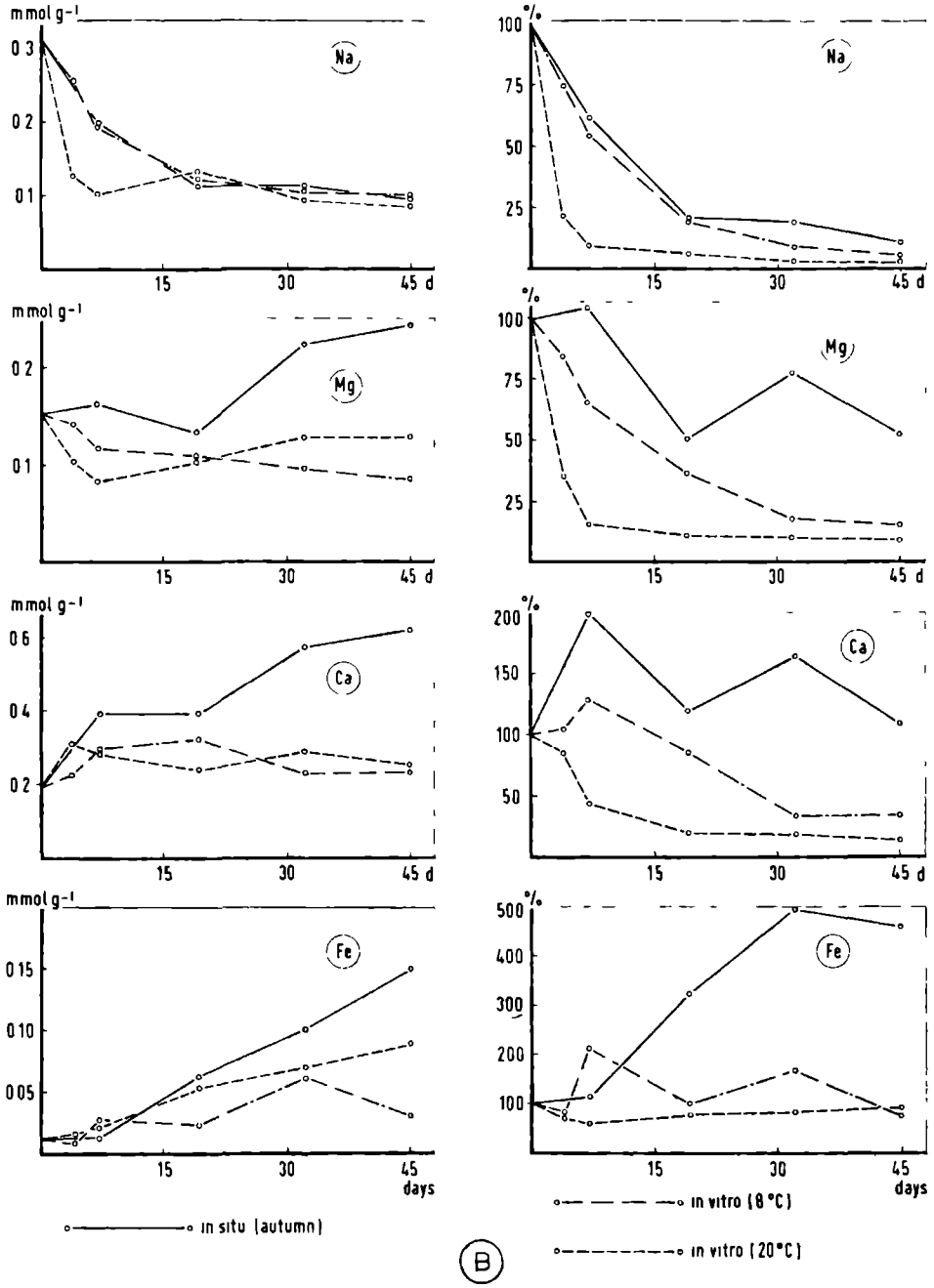

Fig. 5. B. Sodium, magnesium, calcium and iron dynamics during breakdown of *Nymphoides peltata* leaf-blades in the field (solid line) and the laboratory (dotted lines), expressed as mmol per g dry weight (left) and as percentage of the original stock (right) remaining in the litter bags.

and sodium concentrations of the decaying material clearly declined in the first period of the experiment and remained fairly constant later on. In the 20°C temperature-room in particular, there was a fast initial decrease of these nutrients. The relative stocks of phosphorus, potassium and sodium remaining in the litter bags again showed a temperature-dependent decrease. The remaining stock was always somewhat higher in the field than in the 8°C temperature-room.

The magnesium and calcium concentrations of the coarse detritus showed a more or less constant level in the laboratory, while in the field a clear rise in concentration was observed. This increase might also be explained by contamination of the detritus in the field. In the laboratory, the relative stocks of magnesium and calcium showed a temperature-dependent decrease, while the relative stocks of these elements showed irregular patterns in the field.

Both in the field and in the laboratory, the iron concentrations of the coarse detritus increased. However, this increase was more pronounced in the field. The relative stock of iron in the litter bags remained more or less constant in the laboratory and steadily increased in the field.

These observations show that nutrient dynamics of detritus are temperature-dependent. However, care must be taken in interpreting field data obtained with litter bags because of the possibility of contamination of the detritus with "foreign" material.

The colonization of N. peltata *detritus by macro-invertebrates*

Depending on the site and time of incubation, there were qualitative and quantitative differences in the populations of macro-invertebrates which colonized the *N. peltata* detritus in the litter bags (Table III). In general, the number of taxa and the total number of individuals increased during the incubation period. However, a distinct increase in number of taxa was observed in the bags at the *Nymphoides* and open-water site between sampling days 12 and 19. Furthermore, on the last sampling day, a clear decrease in the number of taxa and individuals was observed in the litter bags from the helophyte zone. Although the total number of taxa was at times high, it was found that only a limited number dominated the fauna community in the litter bags. At all sites, the diversity index (H') initially decreased, to increase again later on during the incubation period. The evenness (J') showed a more or less clear decline between sampling days 4 and 31, indicating that in this period, the dominance of a limited number of taxa was more pronounced. More macro-invertebrate taxa were found in the litter bags between the littoral helophytes than in those incubated between *N. peltata*, while the bags from the open water contained the smallest number of taxa. In general, the same was true for the total number of individuals (with the exception of the open-water bags on the last sampling day). The values of the diversity index (H') and the evenness (J') of the macro-invertebrate community in the litter bags were highest between the littoral helophytes, intermediate between *N.*

TABLE III

Number of taxa and individuals of macro-invertebrates found on each sampling day in four litter bags with decomposing leaf-blades of *Nymphoides peltata*

A. BETWEEN HELOPHYTES

Incubation time (days)	4	7	12	19	31	39	Total period
Number of taxa	20	28	23	27	37	28	55
Number of individuals	125	241	333	508	526	245	1973
Shannon–Weaver (H')	3.730	3.663	3.554	3.172	3.340	3.556	3.850
Evenness (J')	0.863	0.762	0.786	0.667	0.641	0.740	0.666
N *Endochironomus* gr. *dispar*	11	56	74	134	103	31	409
Ol *Lumbriculus variegatus* (O.F. Müller)	12	29	36	97	79	65	318
M *Valvata cristata* (O.F. Muller)	1	1	17	83	156	45	303
N *Phaenopsectra* cf. *punctipes* Wied.	2	28	47	65	8		150
N *Glyptotendipes* sp.	12	12	17	2	54	15	112
I *Asellus aquaticus* (L.)	5	7	34	28	17	13	104
Tc *Dugesia polychroa* (O. Schmidt)	8	14	17	12	24	5	80
H *Helobdella stagnalis* (L.)	27	22	6	11	6	2	74
H *Erpobdella octoculata* (L.)	8	14	8	18	6	6	60
M *Bathyomphalus contortus* (L.)		2	38	1	3	6	50
Ol *Tubifex* sp.		11	9	15	11	2	48
Ol *Stylaria lacustris* (L.)	14	23	3	3	1		44
I *Proasellus meridianus* (Racov.)	3	2	8	8	4	2	27
Ol *Limnodrilus* sp.		2		2	1	12	17
N *Ptychoptera contaminata* L.						14	14
M *Planorbis planorbis* (L.)		2	5	1	2	3	13
N *Chironomus* gr. *plumosus* s.l.			2	5	6		13
N *Microtendipes chloris* agg.		1		1	5	4	11
H *Glossiphonia heteroclita* (L.)	2	2		4	1	1	10
B *Eristalis* sp. (larva)	5	1		1	1		8
N *Polypedilum* gr. *nubeculosum* s.l.	2	1	3		2		8
M *Hippeutis complanatus* (L.)				1	4	3	8
N *Endochironomus albipennis* (Meigen)	3	1			3		7
N *Cricotopus* sp.	2	1	1	1		2	7
Ol *Eiseniella tetraeda* Mich.		1	1	3	2		7
Cb *Proisotoma* sp.				3	2	2	7
T *Cyrnus flavidus* McLachlan					6		6
C *Hydroporus* sp. (larva)	1			1	2	1	5
N *Polypedilum gr. sordens*	4						4
C *Enochrus* sp. (larva)	2	1		1			4
N Tipulidae						4	4
N *Xenopelopia* sp.		2			1		3
M *Anisus vortex* (L.)			2		1		3
T *Triaenodes bicolor* (Curtis)					2	1	3
E *Caenis robusta* Eaton					3		3
M *Bithynia leachi* (Sheppard)					2	1	3
N *Parachironomus gr arcuatus*	1	1					2
He *Micronecta minutissima* (L.)		2					2
M *Valvata piscinalis piscinalis* (O.F. Muller)		1				1	2
He *Corixa* sp. (Nymph)			2				2
N *Tanytarsus* sp.			1		1		2
N *Ceratopogonidae*					2		2
Hy *Hydracarina*					2		2
N *Corynoneura* sp.		1					1
Tc *Polycelis tenuis Ijima*			1				1
N *Ablabesmyia longistyla* Fittkau			1				1
M *Radix peregra* (Draparnaud)				1			1
N *Psychoda* sp.				1			1
E *Caenis horaria* (L.)					1		1
B *Notiphila brunnipes* R-D. (larva)					1		1
N *Guttipelopia guttipennis* (Van der Wulp)					1		1
M *Gyraulus albus* (O.F. Müller)						1	1
H *Glossiphonia complanata* (L.)						1	1
C *Helophorus* sp. (larva)						1	1
N *Limnophila* sp.						1	1

TABLE III (continued)

B. BETWEEN NYMPHOIDES

Incubation time (days)	4	7	12	19	31	39	Total period
Number of taxa	17	14	17	24	25	24	47
Number of individuals	104	193	268	270	396	383	1614
Shannon–Weaver (H')	3 451	2.379	3 041	2.814	2.359	3 275	3 530
Evenness (J')	0 844	0.625	0 744	0 614	0 508	0.714	0.636
N *Glyptotendipes* sp.	12	41	94	115	247	106	615
N *Endochironomus albipennis* (Meigen)	21	93	44	15	15		188
H *Helobdella stagnalis* (L.)	6	6	17	19	26	44	118
N Ceratopogonidae	2		32	65			99
Hy Hydracarina					28	65	93
Ol *Stylaria lacustris* (L.)	15	24	9	2	2	9	61
E *Cloeon dipterum* (L.)				2	14	39	55
H *Erpobdella octoculata* (L.)	3	5	15	2	7	13	45
T *Orthotrichia costalis* (Curtis)					2	42	44
T *Cyrnus flavidus* McLachlan	3	1	4	7	4	23	42
N *Polypedilum* gr *nubeculosum* s.l.	4	7	20	5		2	38
N *Phaenopsectra* sp.			9	9	10		28
N *Endochironomus gr dispar*	19		3	1			23
Ol *Tubifex* sp.			10	4	1		15
E *Caenis robusta* Eaton	5	3	1		1	4	14
N *Chironomus gr plumosus* s.l.				1	12	1	14
Ol *Limnodrilus* sp.					9	5	14
N *Parachironomus* gr. *arcuatus*	4	3	4		2		13
M *Valvata piscinalis piscinalis* (O.F. Müller)					2	10	12
N *Ablabesmyia longistyla* Fittkau	1	2	3	3	2		11
N *Polypedilum* gr. *sordens*	2		1	5		2	10
N *Cricotopus* sp.	3	2	1	1			7
M *Gyraulus albus* (O.F. Muller)				1	2	3	6
Ol *Nais simplex* Pignet		4					4
H *Hemiclepsis marginata* (O.F. Muller)				3	1		4
H *Glossiphonia complanata* (L.)				2		2	4
H *Glossiphonia heteroclita* (L.)					1	3	4
M *Valvata cristata* (O.F. Muller)			1	2			3
N *Guttipelopia guttipennis* (Van der Wulp)					3		3
N *Corynoneura* sp	1	1					2
He *Micronecta minutissima* (L.)	2						2
N *Endochironomus tendens* (Fabricius)				2			2
B *Notiphila brunnipes* R-D. (larva)				2			2
M *Bathyomphalus contortus* (L.)				1		1	2
Ol *Lumbriculus variegatus* (O.F. Muller)					2		2
T *Cyrnus crenaticornis* (Kolenati)						2	2
T *Triaenodes bicolor* (Curtis)						2	2
T *Oecetis furva* (Rambur)						2	2
N *Psectrocladius* sp.	1						1
H *Erpobdella testacea* (Savigny)		1					1
I *Asellus aquaticus* (L.)				1			1
E *Caenis horaria* (L.)					1		1
Tc *Dugesia polychroa* (O. Schmidt)					1		1
N *Procladius* sp.					1		1
M *Hippeutis complanatus* (L.)						1	1
M *Lymnaea stagnalis* (L.)						1	1
N *Dicrotendipes gr. nervosus*						1	1

C. OPEN WATER

Incubation time (days)	4	7	13	19	31	39	Total period
Number of taxa	9	8	9	14	18	18	28
Number of individuals	31	114	180	413	345	694	1777
Shannon–Weaver (H')	2.615	1.995	1.741	2 229	2.107	2.595	2.655
Evenness (J')	0.825	0 665	0.549	0.585	0.505	0.622	0.552

TABLE III (continued)

N	*Glyptotendipes* sp.	2	21	33	205	220	251	732
N	*Endochironomus albipennis* (Meigen)	9	59	113	84	35	96	396
N	*Polypedilum* gr *sordens*				19	5	155	179
N	*Cricotopus* sp.	10	21	12	14	10	99	166
N	*Parachironomus gr. arcuatus*	1	2	2	23	27	37	92
N	*Polypedilum* gr. *nubeculosum* s.l.	2	4	12	53	5		76
T	*Cyrnus flavidus* McLachlan			1	3	12	13	29
N	*Dicrotendipes* gr. *nervosus*				1	11	9	21
Ol	*Stylaria lacustris* (L.)	3	2	4	1			10
N	*Endochironomus* gr. *dispar*		4	2		2	1	9
M	*Gyraulus albus* (O.F. Müller)					2	7	9
H	*Erpobdella octoculata* (L)				2	3	3	8
E	*Cloeon dipterum* (L.)					5	3	8
N	Ceratopogonidae				2	2	2	6
T	*Orthotrichia costalis* (Curtis)						6	6
T	*Cyrnus crenaticornis* (Kolenati)					1	3	4
Od	*Ischnura elegans* v.d. L.						4	4
N	*Corynoneura* sp.	1		1	1			3
P	*Bothromesostoma* sp.				3			3
N	*Ablabesmyia longistyla* (Fittkau)				2	1		3
H	*Hemiclepsis marginata* (O.F. Müller)					1	2	3
M	*Radix auricularia* (L.)	2						2
E	*Caenis robusta* Eaton					2		2
Hy	Hydracarina						2	2
H	*Helobdella stagnalis* (L.)	1						1
H	*Piscicola geometra* (L.)		1					1
N	*Phaenopsectra punctipes* Wied.					1		1
N	*Guttipelopia guttipennis* (Van der Wulp)						1	1

B	Brachycera	He	Heteroptera	Od	Odonata
C	Coleoptera	Hy	Hydracarina	Ol	Oligochaeta
Cb	Collembola	I	Isopoda	P	Plathelminthes
E	Ephemeroptera	M	Mollusca	T	Trichoptera
H	Hirudinea	N	Nematocera	Tc	Tricladida

peltata and lowest in the open water. The litter bags from the helophyte zone, especially, contained a relatively large number of taxa which were not found anywhere else (e.g. *Proasellus meridianus*, *Ptychoptera contaminata*, *Planorbis planorbis*, *Microtendipes chloris*), however, these taxa were never dominant. *Endochironomus* gr. *dispar*, *Lumbriculus variegatus*, *Valvata cristata*, *Asellus aquaticus* and *Dugesia polychroa* were the dominant taxa which were found between *N. peltata* detritus in the helophyte zone. Hydracarina, *Cloeon dipterum* and *Orthotrichia costalis* occurred more abundantly in the litter bags from the *N. peltata* zone. More or less dominant taxa of the open water were *Polypedilum* gr. *sordens*, *Cricotopus* spp. and *Parachironomus* gr. *arcuatus*. The litter bags from the *N. peltata* zone had some dominant macro-invertebrate taxa in common with both the litter bags from the helophyte zone (e.g. *Helobdella stagnalis*) and the open water (e.g. *Endochironomus albipennis*). *Glyptotendipes* sp. was dominant at all sites, particularly in the *N. peltata* and open-water zones (Table III).

Figure 6 shows that the Nematocera strongly dominated the macro-invertebrate community of the *N. peltata* detritus at the open-water site. The fauna in and on the detritus in the helophyte zone was more diverse; besides

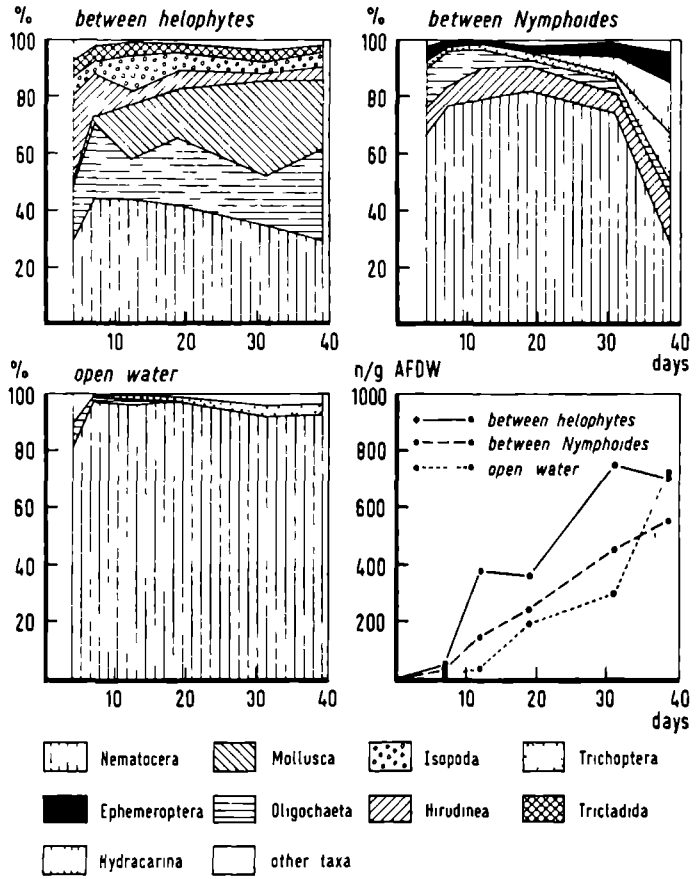

Fig. 6. Relative contributions of various macro-invertebrate groups and total number of macro-invertebrate individuals per g ash-free dry weight of *Nymphoides peltata* detritus at three incubation sites.

Nematocera, other groups could also be found here in relatively high quantities, particularly Oligochaeta and Mollusca. Again, the fauna from the detritus in the *N. peltata* zone showed an intermediate position with respect to the occurrence of different macro-invertebrate groups, but Nematocera were dominant here also. Furthermore, numerous specimens of macro-invertebrates were found at all the sites (up to 750 individuals per g of detritus), particularly in the final stage of the experiment (Fig. 6).

DISCUSSION

Decomposition in aquatic macrophytes generally starts with natural senescence. Natural senescence is an orderly and programmed sequence of events, largely regulated by the plant itself, which leads to the death of plant parts. The lapse of time required for senescence can vary both with the plant

species or plant parts and with environmental conditions (Thimann, 1978). According to Lammens and Van der Velde (1978), decomposition in *N. peltata* can be initiated both by physiological processes of the plant itself, and by external factors such as local damage of leaf-blades, caused, e.g., by animals and pathogens. Epiphytes may also cause the senescence and death of macrophytes (Howard-Williams et al., 1978; Rogers and Breen, 1981). The literature clearly shows that knowledge concerning natural senescence in aquatic macrophytes is scarce. This knowledge, however, is needed to define the actual beginning of decomposition in aquatic macrophytes.

In *Nymphoides peltata*, the different organs senesce with different time constants. Natural senescence of floating leaves of *N. peltata* was a common phenomenon during the entire growing season, so that the input of organic matter into the detrital pool also continued regularly throughout the growing season. The other organs of *N. peltata* played a smaller role in organic matter production and generally showed natural senescence at the end of the growing season only. For the further fate of the plant material, it is crucial when and where it enters the detrital pool, because of the variation in environmental circumstances in space and time. It is shown in the present study that leaf-blade material of *N. peltata* could show significantly different breakdown rates in different seasons and at different sites. Decomposition can be influenced by various environmental factors which show seasonal and spatial variation, such as temperature (e.g. Carpenter and Adams, 1979; this study), nutrient level in the medium (Howarth and Fisher, 1976), turbulence (Federle et al., 1982), light intensity (Blake, 1982) and oxygen concentration (Godshalk and Wetzel, 1978). It is not only important when and where, but also in what condition, plant parts enter the detrital pool. Physiologically young and old plant parts of the same type which enter the detrital pool can show different breakdown patterns (Harrison and Mann, 1975; Bastardo, 1979; Blake, 1982; this study). These differences are most probably dependent on chemical variation in the plant material. In this respect, it is worth mentioning that processes like resorption and translocation of nutrients and organic matter normally occur in senescing leaves which are still connected to the plant. In nearly all decomposition studies (including the present one), however, mature but isolated plant parts were used to describe breakdown; these studies more or less simulate the decay of plant parts which are detached, e.g. due to the activities of animals or storm.

In the present study, it was found that different plant parts of *N. peltata* could have significantly different breakdown rates. Literature data on weight loss of coarse macrophyte detritus also show differences between different plant parts (Bastardo, 1979; Howard-Williams et al., 1983; Esteves and Barbieri, 1983). In general, data on the weight loss from aquatic macrophytes show large interspecific variations; the breakdown rates of *N. peltata* plant parts as found in the present study are among the fastest in the range reported in the literature (Godshalk and Wetzel, 1978; Bastardo, 1979; Howard-Williams and Davies, 1979; Hill and Webster, 1982; Kulshreshtha

and Gopal, 1982). The overall rate of decomposition of macrophyte material is primarily a function of the chemical composition of the plant material. Plant materials rich in, e.g., cross-linked celluloses, lignins and paracoumaric esters resist decay, while those with polymers of lesser structural complexity, and with a larger proportion of hydrolysable components, are more easily degraded (Suberkropp et al., 1976; Boon et al., 1982). According to Godshalk and Wetzel (1978) and Carpenter and Adams (1979), weight loss rates during decomposition correlate with initial levels of nitrogen in the plant material. In *N. peltata*, however, a clear correlation between initial C/N ratio and the breakdown of plant parts could not be found, particularly when the decay of underground organs is compared with above-ground plant parts.

In the present study, it was found that ca. 5—6% of the coarse leaf-blade detritus of *N. peltata* disappeared as a result of autolysis and 18—23% as a result of physical leaching of organic substances. This percentage of physical leaching comes close to that found by Federle and Vestal (1982) for *Carex* litter (ca. 19—20%). Polunin (1982) estimated the physical leaching to be ca. 13% of the total breakdown in *Phragmites* leaves. So there appears to be some interspecific variation in the leachable fraction of aquatic macrophytes.

Most of the disappearance of *N. peltata* detritus can be attributed to micro-organisms. According to Lammens and Van der Velde (1978), the parasitic fungus *Septoria villarsiae* Desm. is an important decomposer of *N. peltata* leaf-blades as long as these organs still float on the water surface. In the present study, observations were made on the decay of *N. peltata* leaf-blades under water. It was found that in the initial phase of the decomposition under water, bacteria were far more important than fungi in the breakdown of coarse *Nymphoides* detritus. Later on, the role of the fungi in the disappearance of the coarse *Nymphoides* detritus increased (Fig. 4). Kaushik and Hynes (1971) found that in water, fungi were far more important in the initial decay period of *Ulmus* leaves than were bacteria. Mason (1976) showed that in water, bacteria were as important as fungi in both the weight loss and microbial respiration in dead *Phragmites* leaves over a considerable length of time. According to Rublee and Roman (1982), bacteria are not as effective as fungi in hydrolysing structural carbohydrates rapidly. Therefore, differences in the relative contributions of bacteria and fungi to the breakdown of plant material in the medium water might partly be due to differences in chemical properties of the detritus. However, environmental conditions can also be of importance; thus a shift from bacterial to fungal decomposition may occur with decreasing pH (Hendrey et al., 1976). Although it is generally accepted that bacteria and fungi play an important role in the decomposition of aquatic macrophytes, these organisms are rarely identified. From decomposing *N. peltata* leaves of experiments described in the present study, some pythiaceous fungi were isolated which were recorded for the first time in The Netherlands, viz., *Pythium pleroticum* T. Ito, *Pythium apleroticum* Tokunaga and *Pythium marsipium* Drechsler. Furthermore, the Oomycetes *Pythium diclinum* Tokunaga, *Pythium* 'F' and *Sapro-*

legnia ferax (Gruith.) Thuret were found between the *N. peltata* detritus (see Jacobs, 1982). Although it appeared that bacteria were very important in the initial decay period of *N. peltata*, no data on their taxonomic status are available.

In the present study, it was found that the various elements incorporated in *N. peltata* leaves disappeared at different rates during decomposition. In the laboratory, the net loss rates of the various elements in the coarse detritus showed the following order: K>Na>P>Mg>C>N>Ca>Fe. The loss-rate of a particular nutrient is certainly influenced by the way it is incorporated in the organic matter. Several studies have indicated that elements such as potassium and sodium are loosely bound in plant material, and that these elements are the first ones to be lost during decomposition (see Davis and Van der Valk, 1978; Kulshreshtha and Gopal, 1982). A relatively low rate of disappearance of a particular nutrient can be explained by a relatively faster breakdown of plant material with a low content of that nutrient. In addition, adsorption processes, contamination (e.g. by sediment particles) and the biomass and excretions of organisms can cause an enrichment of detritus with certain elements. The considerable enrichment of the *N. peltata* detritus with iron, calcium and magnesium in the field can most probably be attributed to precipitation and contamination. The increase in nitrogen content of detritus can, at least partially, be attributed to an increase in microbial biomass (Fenchel, 1970) and extracellular excretions of microbes (Robinson et al., 1982), and to chemical binding of nitrogeneous substances to certain detritus fractions, e.g. lignins (Triska and Sedell, 1976).

Macro-invertebrate densities on *N. peltata* detritus in the Bemmelse Strang were high when compared with the densities recorded from other investigations of macrophyte and tree-leaf breakdown in aquatic systems (see e.g. Winterbourn, 1978; Danell and Sjöberg, 1979; Smock and Stoneburner, 1980; Pidgeon and Cairns, 1981; Dudgeon, 1982; Hill and Webster, 1982; Hanlon, 1982; Mutch et al., 1983). These studies also indicate that there are many factors which influence the numbers of macro-invertebrates in and on detritus enclosed in litter bags, e.g., exposure time, the type of detritus, the type of the water body, the season, the incubation site within a lake, the surface area and shelter offered by the bags, and the amount of plant material enclosed. In the present study, it was found that not only detrivores (facultative or obligate), but also carnivores such as leeaches, triclads and water mites, colonized the *N. peltata* detritus. This may be explained by the high densities of potential prey animals that occurred in the bags.

Macro-invertebrates can play several roles in the decomposition of aquatic macrophytes, such as fragmentation of the coarse detritus, the mixing of macrophyte detritus with sediment material and the feeding on the detritus. Detritivores utilize microbes in preference to the ingested dead detritus, and thus their feeding is dependent on microbial conditioning of the detritus (e.g. Kaushik and Hynes, 1971). Furthermore, macro-invertebrate feeding on microbes attached to detritus has been shown to stimulate decomposition

(e.g. Barsdate et al., 1974; Lopez et al., 1977; Fish and Carpenter, 1982). According to Barsdate et al. (1974), detritivores can keep microbes physiologically young and growing rapidly, so that the decomposition is stimulated.

The decomposition processes associated with *N. peltata* detritus discussed here not only result in mineralization of the organic matter, but also in a transformation of coarse plant material into fine particulate and dissolved organic matter (partly resisting further decay). The decomposing plant parts of *N. peltata* showed a very fast fragmentation into smaller particles and diffuse material; only trichosclereids, parts of the major veins, and fragments of the epidermis with hydropote cells (if any) remained recognizable for a fairly long time. Although the fine particulate and dissolved organic matter could constitute a considerable fraction of the total organic carbon pool of *N. peltata* detritus, both the coarse detritus and the total organic carbon of *N. peltata* leaves showed a relatively high rate of disappearance.

As stated above, decomposition of macrophyte material is a very complex process, including not only changes in and loss of organic matter, but also interactions between detritus and decomposers. It is evident that *Nymphoides peltata* detritus plays an important role as habitat and/or as food for many organisms in the system studied. However, the more specific relations between these organisms and *Nymphoides* detritus, as well as the nature of the changes in organic matter during decomposition, largely remain to be investigated.

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REFERENCES

Bärlocher, F. and Kendrick, B., 1975. Leaf-conditioning by microorganisms. Oecologia (Berlin), 20: 395–362.

Barsdate, R.J., Prentki, R.T. and Fenchel, T., 1974. Phosphorus cycle of model ecosystems: significance for decomposer food chains and effects of bacterial grazers. Oikos, 25: 239–251.

Bastardo, H., 1979. Laboratory studies on decomposition of littoral plants. Pol. Arch. Hydrobiol., 26: 267–299.

Blake, G., 1982. Characterization of decomposition of plant material in an alpine lake. Hydrobiol. Bull. (Amsterdam), 16: 5–9.

Boon, J.J., Wetzel, R.G. and Godshalk, G.L., 1982. Pyrolysis mass spectrometry of some *Scirpus* species and their decomposition products. Limnol. Oceanogr., 27: 839–848.

Brock, Th.C.M., 1983. The distribution of elements in a *Nymphoides peltata*-dominated system. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18—23 September 1983, pp. 41—45.

Brock, Th.C.M., Huijbrechts, C.A.M., Van de Steeg-Huberts, M.J.H.A. and Vlassak, M.A., 1982. In situ studies on the breakdown of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae); some methodological aspects of the litter bag technique. Hydrobiol. Bull. (Amsterdam), 16: 35—49.

Brock, Th.C.M., Arts, G.H.P., Goossen, I.L.M. and Rutenfrans, A.H.M., 1983a. Structure and annual biomass production of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae). Aquat. Bot., 17: 167—188.

Brock, Th.C.M., Bongaerts, M.C.M., Heijnen, G.J.M.A. and Heijthuijsen, J.H.F.G., 1983b. Nitrogen and phosphorus accumulation and cycling by *Nymphoides peltata* (Gmel.)O. Kuntze (Menyanthaceae). Aquat. Bot., 17: 189—214.

Carpenter, S.R. and Adams, M.S., 1979. Effects of nutrients and temperature on decomposition of *Myriophyllum spicatum* L. in a hard water eutrophic lake. Limnol. Oceanogr., 24: 520—528.

Danell, K. and Sjöberg, K., 1979. Decomposition of *Carex* and *Equisetum* in a northern Swedish lake: dry weight loss and colonization by macro-invertebrates. J. Ecol., 67: 191—200.

Davis, C.B. and Van der Valk, A.G., 1978. The decomposition of standing and fallen litter of *Typha glauca* and *Scirpus fluviatilis*. Can. J. Bot., 56: 662—675.

Dudgeon, D., 1982. An investigation of physical and biological processes of two species of leaf litter in Tai Po Kau Forest Stream, New Territories, Hong Kong. Arch. Hydrobiol., 96: 1—32.

Esteves, F.A. and Barbieri, R., 1983. Dry weight and chemical changes during decomposition of tropical macrophytes in Lobo Reservoir, São Paulo, Brazil. Aquat. Bot., 16: 285—295.

Federle, T.W. and Vestal, J.R., 1980. Microbial colonization and decomposition of *Carex* litter in an arctic lake. Appl. Environ. Microbiol., 39: 888—893.

Federle, T.W. and Vestal, J.R., 1982. Evidence of microbial succession on decaying leaf litter in an arctic lake. Can. J. Microbiol., 28: 686—695.

Federle, T.W., McKinley, V.L. and Vestal, J.R., 1982. Physical determinants of microbial colonization and decomposition of plant litter in an arctic lake. Microb. Ecol., 8: 127—138.

Fenchel, T.M., 1970. Studies on the decomposition of organic detritus derived from the turtle grass *Thalassia testudinum*. Limnol. Oceanogr., 15: 14—20.

Fenchel, T.M. and Jørgensen, B.B., 1977. Detritus food chains of aquatic ecosystems. The role of bacteria. In: M. Alexander (Editor), Advances in Microbial Ecology. Vol. I. Plenum Press, New York, pp. 1—58.

Fish, D. and Carpenter, S.R., 1982. Leaf litter and larval mosquito dynamics in tree-hole ecosystems. Ecology, 63: 283—288.

Godshalk, G.L. and Wetzel, R.G., 1978. Decomposition of aquatic angiosperms. II. Particulate components. Aquat. Bot., 5: 301—327.

Hanlon, R.D.G., 1982. The breakdown and decomposition of allochthonous and autochthonous plant litter in an oligotrophic lake (Lake Frongoch). Hydrobiologia, 88: 281—288.

Harrison, P.G. and Mann, K.H., 1975. Detritus formation from eelgrass (*Zostera marina*): The relative effects of fragmentation, leaching and decay. Limnol. Oceanogr., 20: 924—934.

Hendrey, G.R., Baalsrud, K., Traaen, T., Laake, M. and Raddum, G., 1976. Acid precipitation: some hydrobiological changes. Ambio, 5/6: 224—227.

Hill, B.H. and Webster, J.R., 1982. Aquatic macrophyte breakdown in an Appalachian river. Hydrobiologia, 89: 53—59.

Howard Williams, C and Davies, B R , 1979 The rates of dry matter and nutrient loss from decomposing *Potamogeton pectinatus* in a brackish south temperate coastal lake Freshwater Biol , 9 13—21

Howard Williams, C , Davies, B R and Cross, R H M , 1978 The influence of periphyton on the surface structure of a *Potamogeton pectinatus* L leaf (an hypothesis) Aquat Bot , 5 87—91

Howard Williams, C , Pickmere, S and Davies, J , 1983 Decay rates and nitrogen dynam ics of decomposing watercress (*Nasturtium officinale* R Br) Hydrobiologia, 99 207—214

Howarth, R W and Fisher, S G , 1976 Carbon, nitrogen, and phosphorus dynamics during leaf decay in nutrient enriched stream micro ecosystems Freshwater Biol , 6 221—228

Jacobs, R P W M , 1982 Pythiaceous fungi associated with the decomposition of *Nym phoides peltata* Antonie van Leeuwenhoek, 48 433—445

Kaushik, N K and Hynes, H B N , 1971 The fate of dead leaves that fall into streams Arch Hydrobiol , 68 465—515

Kotz, L , Kaiser, G , Tschopel, P and Tolg, G , 1972 Aufschluss biologischer Matrices fur die Bestimmung sehr niedriger Spurenelementgehalte bei begrenzter Einwaage mit Salpetersaure unter Druck in einem Teflongefass Z Anal Chem , 260 207—209

Kulshreshtha, M and Gopal, B , 1982 Decomposition of freshwater wetland vegetation I Submerged and free floating macrophytes In B Gopal, R E Turner, R G Wetzel and D F Whigham (Editors), Wetlands Ecology and Management International Science Publishers, Jaipur, pp 259—278

Lammens, E H R R and Van der Velde, G , 1978 Observations on the decomposition of *Nymphoides peltata* (Gmel)O Kuntze (Menyanthaceae) with special regard to the leaves Aquat Bot., 4 331—346

Lopez, G R , Levinton, J S and Slobodkin, L B , 1977 The effect of grazing by the detritivore *Orchestra grillus* on *Spartina* litter and its associated microbial community Oecologia (Berlin), 30 111—127

Mason, C F , 1976 Relative importance of fungi and bacteria in the decomposition of *Phragmites* leaves Hydrobiologia, 51 65—69

Mutch, R A , Steedman, R J , Berte, S B and Pritchard, G , 1983 Leaf breakdown in a mountain stream, a comparison of methods Arch Hydrobiol , 97 89—108

Olson, J S , 1963 Energy storage and the balance of producers and decomposers in ecological systems Ecology, 44 322—331

Pidgeon, R W J and Cairns, S C , 1981 Decomposition and colonization by invertebrates of native and exotic leaf material in a small stream in New England (Australia) Hydro biologia, 77 113—127

Polunin, N V C , 1982 Processes contributing to the decay of reed (*Phragmites australis*) litter in fresh water Arch Hydrobiol , 94 182—209

Rice, D L and Tenore, K R , 1981 Dynamics of carbon and nitrogen during the decom- position of detritus derived from estuarine macrophytes Estuarine, Coastal Shelf Sci , 13 681—690

Robinson, J D , Mann, K H and Novitsky, J A , 1982 Conversion of the particulate fraction of seaweed detritus to bacterial biomass Limnol Oceanogr , 27 1072—1079

Roelofs, J G M , 1983 An instrumental method for the estimation of organic carbon in seston, macrophytes and sediments Aquat Bot , 16 391—397

Rogers, K H and Breen, C M , 1981 Effects of epiphyton on *Potamogeton crispus* L leaves Microb Ecol , 7 351—363

Rogers, K H and Breen, C M , 1982 Decomposition of *Potamogeton crispus* L the ef- fect of drying on the pattern of mass and nutrient loss Aquat Bot , 12 1—12

Rublee, P A and Roman, M R , 1982 Decomposition of turtlegrass (*Thalassia testudi num* Konig) in flowing sea water tanks and litter bags, compositional changes and comparison with natural particulate matter J Exp Mar Biol Ecol , 58 47—58

Scheffé, H., 1959. The Analysis of Variance. A Wiley Publication in Mathematical Statistics. Wiley, New York, 477 pp.

Smock, L.A. and Stoneburner, D.L., 1980. The response of macro-invertebrates to aquatic macrophyte decomposition. Oikos, 35: 397—403.

Suberkropp, K.F., Godshalk, G.L. and Klug, M.J., 1976. Changes in the chemical composition of leaves during processing in a woodland stream. Ecology, 57: 720—727.

Thimann, K.V., 1978. Senescence. Bot. Mag. Tokyo, Special Issue, 1: 19—43.

Triska, F.J. and Sedell, J.R., 1976. Decomposition of four species of leaf litter in response to nitrate manipulation. Ecology, 57: 783—792.

Van der Velde, G., 1980. Studies in nymphaeid-dominated systems with special emphasis on those dominated by *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae). Thesis, Nijmegen, 163 pp.

Van der Velde, G., Giessen, Th.G. and Van der Heijden, L., 1979. Structure, biomass and seasonal changes in biomass of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae), a preliminary study. Aquat. Bot., 7: 279—300.

Van der Velde, G., Van der Heijden, L.A., Van Grunsven, P.A.J. and Bexkens, P.M.M., 1982. Initial decomposition of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae), as studied by the leaf-marking method. Hydrobiol. Bull. (Amsterdam), 16: 51—60.

Van der Velde, G., Van der Heijden, L.A., Van Grunsven, P.A.J. and Bexkens, P.M.M., 1984. Development and productivity of the floating leaves of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae). Aquat. Bot., submitted for publication.

Winterbourn, M.J., 1978. An evaluation of the mesh bag method for studying leaf colonization by stream invertebrates. Verh. Int. Verein. Limnol., 20: 1557—1561.

Aquatic Botany, 21 (1985) 1—22
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FIELD STUDIES ON THE BREAKDOWN OF *NUPHAR LUTEA* (L.)SM. (NYMPHAEACEAE), AND A COMPARISON OF THREE MATHEMATICAL MODELS FOR ORGANIC WEIGHT LOSS

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ABSTRACT

Brock, Th.C.M., De Lyon, M.J.H., Van Laar, E.M.J.M. and Van Loon, E.M.M., 1985. Field studies on the breakdown of *Nuphar lutea* (L.)Sm. (Nymphaeaceae), and a comparison of three mathematical models for organic weight loss. *Aquat. Bot.*, 21: 1—22.

Aspects of the decomposition of the aquatic macrophyte *Nuphar lutea* (L.)Sm. were studied using the litter bag method in the field. The organic weight loss during breakdown was described by means of 1 simple and 2 composite exponential models. The nitrogen, phosphorus and potassium concentrations of the remaining detritus were analysed.

The composite exponential models fitted the decay data better than the "simple exponential function". However, it was difficult to interpret the individual estimates of the composite exponential models in terms of overall decay.

The patterns of organic weight loss and nutrient dynamics of decomposing *Nuphar lutea* depended on which part of the plant was being studied. In general, the aboveground plant parts showed a faster organic weight loss and a faster nutrient release than the underground structures. The breakdown of *Nuphar lutea* leaves was considerably faster in summer than in autumn. The organic weight loss and nutrient dynamics of the decomposing leaves were influenced by the trophic status of the system. Particularly in an acid moorland pool the breakdown of the leaves was relatively slow when compared to that of an eutrophicated system and an alkaline oxbow lake. The effect of the litter bag mesh size (0.27 and 0.78 mm) on the breakdown of the leaves was relatively small.

INTRODUCTION

The Netherlands abound in small, shallow aquatic ecosystems. The role of vascular plants in many of these systems is very important because they can form the community frame of the system and comprise the major source of organic matter. The project on the structure and functioning of macrophyte-dominated systems (Den Hartog, 1978, 1983) includes

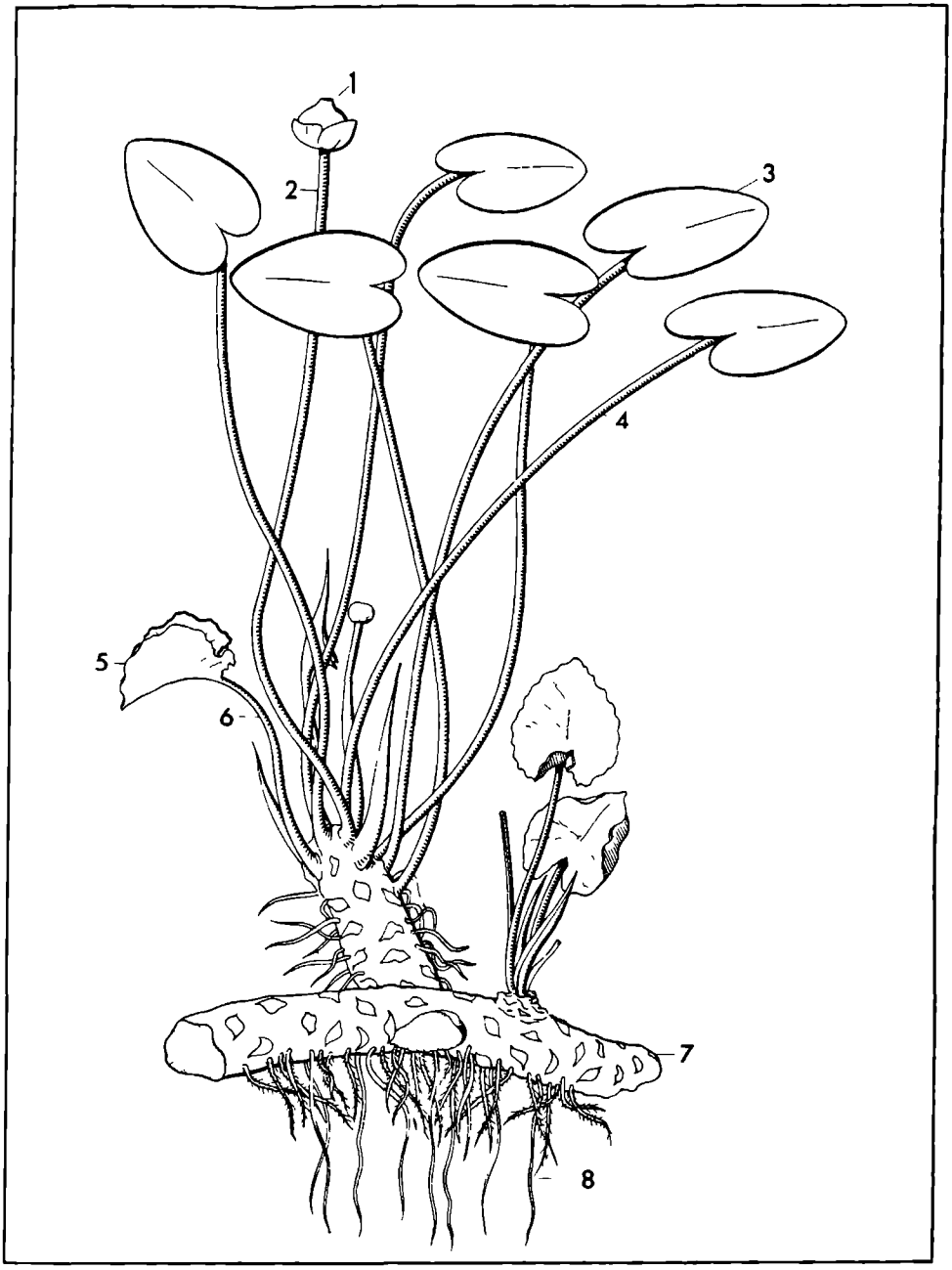

Fig. 1. *Nuphar lutea* (L.)Sm. and its various plant parts: flowers/fruits (1), peduncles (2), laminae of floating leaves (3), laminae of submerged leaves (5), petioles (4 and 6), root stocks (7) and roots (8).

the study of systems dominated by nymphaeids (Van der Velde, 1980). Nymphaeids, such as *Nuphar lutea* (L.)Sm., are aquatic plants which root in the bottom and possess mainly floating leaves (see Fig. 1). Recently, several case studies on structural and functional aspects of *Nuphar lutea* have been published. These case studies dealt with biomass production (Van der Velde and Peelen-Bexkens, 1983), floral biology (Giesen and Van der Velde, 1983), associated macro-invertebrates (Van der Velde, 1978; Brock and Van der Velde, 1983), associated epiphytes (Delbecque, 1983; Delbecque and Chatrou, 1983) and effects on phytoplankton (Roijackers, 1983, 1984). The underlying assumption is that by studying several aspects of the nymphaeid-dominated system separately, but also in relation to each other, it should be possible to arrive at a reasonable structural and functional model of the system as a whole (Van der Velde, 1980). The present paper deals with aspects of the decomposition of *Nuphar lutea*.

Nuphar lutea can be a productive macrophyte in a wide range of lakes (see e.g., Van der Velde and Peelen-Bexkens, 1983). Only a relatively small proportion of the biomass produced by *Nuphar lutea* is grazed by herbivores and consequently most material senesces and is subject to physical (leaching, fragmentation) and biochemical (autolysis, microbial enzymes) breakdown. Knowledge of the decomposition of *Nuphar lutea* detritus is essential for an understanding of the ecological significance of this macrophyte in the systems studied.

A general approach to the analysis of data concerning organic weight loss of plant material during breakdown is the fitting of mathematical models to these data in order to estimate breakdown rates of the detritus (for a detailed discussion see Wieder and Lang, 1982). The most frequently used model to describe decomposition of macrophytes is the "simple exponential model" discussed in detail by Olsen (1963). However, De Lyon et al. (1983) demonstrated that in the laboratory the breakdown of coarse *Nuphar lutea* detritus was better described by means of certain composite exponential models, such as those described by Lousier and Parkinson (1976) and Godshalk and Wetzel (1978). Therefore, in the present paper both the "simple exponential function" and some composite exponential models are used to describe the breakdown of *Nuphar lutea* in the field.

The general objectives of the present paper are: to describe the breakdown of the different morphological structures of *Nuphar lutea* under natural circumstances; to describe the organic weight loss and nitrogen, phosphorus and potassium dynamics of decomposing *Nuphar lutea* leaves in 3 aquatic systems, which differ in pH, alkalinity and nutrient level.

STUDY SITES

The present study was conducted in 4 shallow aquatic systems in the Netherlands, in which *Nuphar lutea* locally dominated the vegetation;

these were: the Bemmelse Strang; the Oude Waal; the Grote Vilt, and the Voorste Choorven.

The Bemmelse Strang and the Oude Waal are 2 backwaters of the river Waal, which are nearly identical in hydrology and water chemistry. These eutrophic, alkaline oxbow lakes are situated in the river forelands, north of the city of Nijmegen (Province of Gelderland). The water depth and water chemistry of these oxbow lakes are strongly influenced by the river Waal (see Brock et al., 1983) particularly in winter and spring.

The Grote Vilt is an oxbow lake of the river Meuse and is situated near the village of Beugen (Province of Noord-Brabant). The water of this lake is medium-alkaline and rich in nutrients, due to eutrophication. During the investigation period blooms of bluegreen algae were regularly observed. The hydrology of the lake is mainly dependent on rain and ground water.

The Voorste Choorven is a moorland pool near Oisterwijk (Province of Noord-Brabant), the hydrology of which is mainly dependent on rainfall. During the last decades the water of this moorland pool, which has a poorly buffered sandy soil, has acidified due to acid precipitation.

MATERIALS AND METHODS

The decomposition of *Nuphar lutea* in the field was studied with the litter-bag (mesh bag) technique. Polyethylene litter bags (35 × 35 cm) with a 0.27 and 0.78 mm mesh size were used. It has been found in preliminary studies that detritivores such as chironomids could enter the bags with a 0.78 mm mesh size, but had more difficulties invading those with a 0.27 mm mesh size. The material retained by these litter bags is defined in the present paper as coarse detritus. In the *Nuphar* material harvested, the different morphological structures (Fig. 1) of the plant were separated where necessary. The more or less undamaged, mature *Nuphar* plant parts were washed, and placed for a few seconds between filter paper to remove excess water. Then the material of each morphological structure was divided into equal portions, weighed and enclosed in the litter bags. The initial fresh weight of the material enclosed in each litter bag was printed on a rotex tape, which was placed in the litter bag. Depending upon the type of plant part, portions of ca. 200—300 g fresh weight were enclosed in the litter bags. At least 10 specimens from each plant part were usually enclosed in the bags, in order to obtain comparable samples. However, the root-stock litter bags only contained four 15-cm-long sections of root-stock because they were too small to contain the root-stock entirely. Fresh material was used in the decomposition experiments because pre-drying of plant material affects weight loss and nutrient release (Brock et al., 1982; Larsen, 1982; Rogers and Breen, 1982). Dry weight and ash- and nutrient-content of the *Nuphar* material enclosed in the bags were estimated at the beginning of each experiment from 5 replicate samples.

The experiment, which was designed to simulate the natural decom-

position of the different plant parts of *Nuphar lutea*, was performed in the Bemmelse Strang (starting on 18 September 1981). The bags with laminae of floating and submerged leaves and those with petioles were allowed to float near the surface of the water at the study site until they became water-logged and sank to the bottom. The bags with the root stocks were anchored to the bottom, while those with the roots were buried in the sediment of the *Nuphar* stands. For all plant parts, the mesh size of the litter bags used was 0.27 mm. Furthermore, a series of litter bags with a 0.78-mm mesh size, in which laminae of floating leaves were enclosed, was incubated at the same time and place as the corresponding 0.27-mm series. After 4, 11, 24, 45 and 137 days 5 litter bags of each series, containing a particular plant part, were retrieved from the study site. However, on the last sampling day some bags of certain plant parts could no longer be found.

To study the influence of environmental factors on the breakdown of *Nuphar lutea*, litter bags (0.27-mm mesh size) with laminae of floating leaves were incubated in 3 aquatic systems with a different trophic status, viz., the Oude Waal, the Grote Vilt and the Voorste Choorven. The collecting of the plant material as well as the incubation were performed in the same system. Apart from the 0.27-mm litter bags, another series of bags with a 0.78-mm mesh size was incubated in the Oude Waal. This experiment started on 6 July 1982 and after 7, 14, 28, 42, 62 and 105 days of incubation 5 bags with decaying leaves from each series were retrieved from the 3 study sites. In addition, on each sampling day water samples of the Oude Waal, the Grote Vilt and the Voorste Choorven were collected for nutrient analyses. Furthermore, the minimum and maximum temperatures, the pH, and alkalinity of the water from these study sites were measured on each sampling day. A detailed description of the sample processing in the laboratory is given by Brock (1984). The nutrient analyses of the water and plant material were performed according to the methods described in Brock et al. (1983).

MATHEMATICAL ANALYSES

For each litter bag incubated in one of the study sites, the fresh weight (*FW*) of the enclosed *Nuphar* material was determined at the start ($t0$) of each experiment. The relative residual ash-free dry weight (*AFDW*) of the plant material in each litter bag, sampled on a particular day (ti), was calculated by means of the quotient:

$$\frac{AFDW(\text{bag } ti) \text{ on } t0}{AFDW(\text{bag } t0) \text{ on } t0}$$

The *AFDW* value of bag ti on $t0$ was estimated from the initial *FW* of

the plant material in bag *ti*, and the *AFDW* values of the *Nuphar* material in the bags sampled on *t*0, i.e.;

$$\frac{AFDW(\text{bag } ti) \text{ on } t0}{AFDW(\text{bag } t0) \text{ on } t0} \times \frac{FW(\text{bag } t0) \text{ on } t0}{FW(\text{bag } ti) \text{ on } t0} = 1$$

$$\frac{AFDW(\text{bag } ti) \text{ on } ti}{FW(\text{bag } ti) \text{ on } t0} : \frac{AFDW(\text{bag } t0) \text{ on } t0}{FW(\text{bag } t0) \text{ on } t0} = \text{relative residual } AFDW$$

Thus, the values obtained for residual organic weight of the different experiments and treatments were compared statistically for each sampling day by using the 1-way analysis of variance and Scheffé's simultaneous test (Scheffé, 1959). Furthermore, 3 different mathematical models were fitted to the decomposition data by using an IBM computer and by applying SAS program NLIN (Goodnight, 1979). The mathematical models used were: the "simple exponential function" (Jenny et al., 1949; Olson, 1963); the "decaying coefficient function" (Godshalk and Wetzel, 1978), and the "2 component function" (Lousier and Parkinson, 1976; Carpenter, 1982).

The "simple exponential function" is of the type;

$$W(t) = W(0) \cdot \exp(-k \cdot t)$$

which is the solution of $dW/dt = -k \cdot W$, where $W(t)$ is the mass remaining after a time interval t (in the present paper measured in days), $W(0)$ is the initial mass, exp is the base of the natural logarithm, and k is the rate constant. In this model it is assumed that during breakdown relatively simple compounds of detritus (e.g., sugars) will be rapidly utilized by decomposers and that more persistent materials (e.g. lignin) will be lost at relatively slower rates, but, in such a way that the relative decomposition rate remains constant.

The "decaying coefficient model" is a modification of the first model ($dW/dt = -k \cdot W$), where k is considered to decrease exponentially ($k = a \cdot \exp(-b \cdot t)$) i.e.,

$$W(t) = W(0)\exp(a(\exp(-b \cdot t)-1)/b).$$

The Parameter a is the decay coefficient at Day 0, and Parameter b is the constant proportion by which Parameter k changes during each time interval. In this model it is also assumed that the relative proportion of persistent components in the detritus increases with time, but in such a way that the relative decomposition rate decreases exponentially.

The "2 component function" is of the type,

$$W(t) = (W(0)-R) \cdot \exp(-KL \cdot t) + R \cdot \exp(-KR \cdot t)$$

where R is the refractory component of the initial plant material, $W(0)-R$ the labile portion, KR the rate constant of R and KL the rate constant

of $W(0)$-R. In this model, it is assumed that plant material can be partitioned into 2 components, a relatively labile fraction ($W(0)$-R), and a more persistent fraction (R), and that each fraction decays exponentially.

The breakdown rates obtained from the above-mentioned functions for the different treatments were statistically compared by means of the Student's t-test.

RESULTS

Organic weight loss

It was found that in the course of the experiment not all the root-stock parts incubated showed senescence and death in all litter bags. Apparently the physiological condition of the incubated root-stock material varied considerably, which also explains the very high standard deviations of the residual weight data (Fig. 2B). However, all other plant parts incubated showed senescence and decomposition from the start. A comparison of the relative amounts of residual organic mass of the various plant parts of *Nuphar lutea* reveals differences in breakdown patterns between most organs, except between roots and root-stocks (Fig. 2, Table IA). On the

TABLE I

A statistical comparison (1-way ANOVA and Scheffé's simultaneous test) of the values of residual weight of the various decomposing *Nuphar lutea* plant parts on each sampling day

	Sampling day[a]					
	*T*1	*T*2	*T*3	*T*4	*T*5	*T*6
A. Floating leaves/submerged leaves	+	+	+	+		
Floating leaves/petioles	–	–	+	–	+	
Floating leaves/root-stocks	–	–	–	+	+	
Floating leaves/roots	–	–	+	+	+	
Submerged leaves/petioles	+	+	+	+		
Submerged leaves/root-stocks	–	–	+	+		
Submerged leaves/roots	+	+	+	+		
Petioles/root-stocks	–	–	–	+	+	
Petioles/roots	–	–	–	+	+	
Root-stocks/roots	–	–	–	–	–	
B. Autumn 0.27 mm/autumn 0.78 mm	–	–	–	–	+	
Summer 0.27 mm/summer 0.78 mm	–	–	–	+	–	
C. Oude Waal/Grote Vilt	–	–	–	–	–	–
Oude Waal/Voorste Choorven	+	+	+	+	+	–
Grote Vilt/Voorste Choorven	+	+	+	+	+	–

[a]+, Significantly different ($P < 0.05$); , not significantly different ($P > 0.05$).

last sampling days, the relative amounts of residual organic mass of the aboveground plant parts were smaller than the residual quantities of the underground organs, indicating a slower breakdown of roots and root stocks. Furthermore, on each sampling day the amount of residual mass

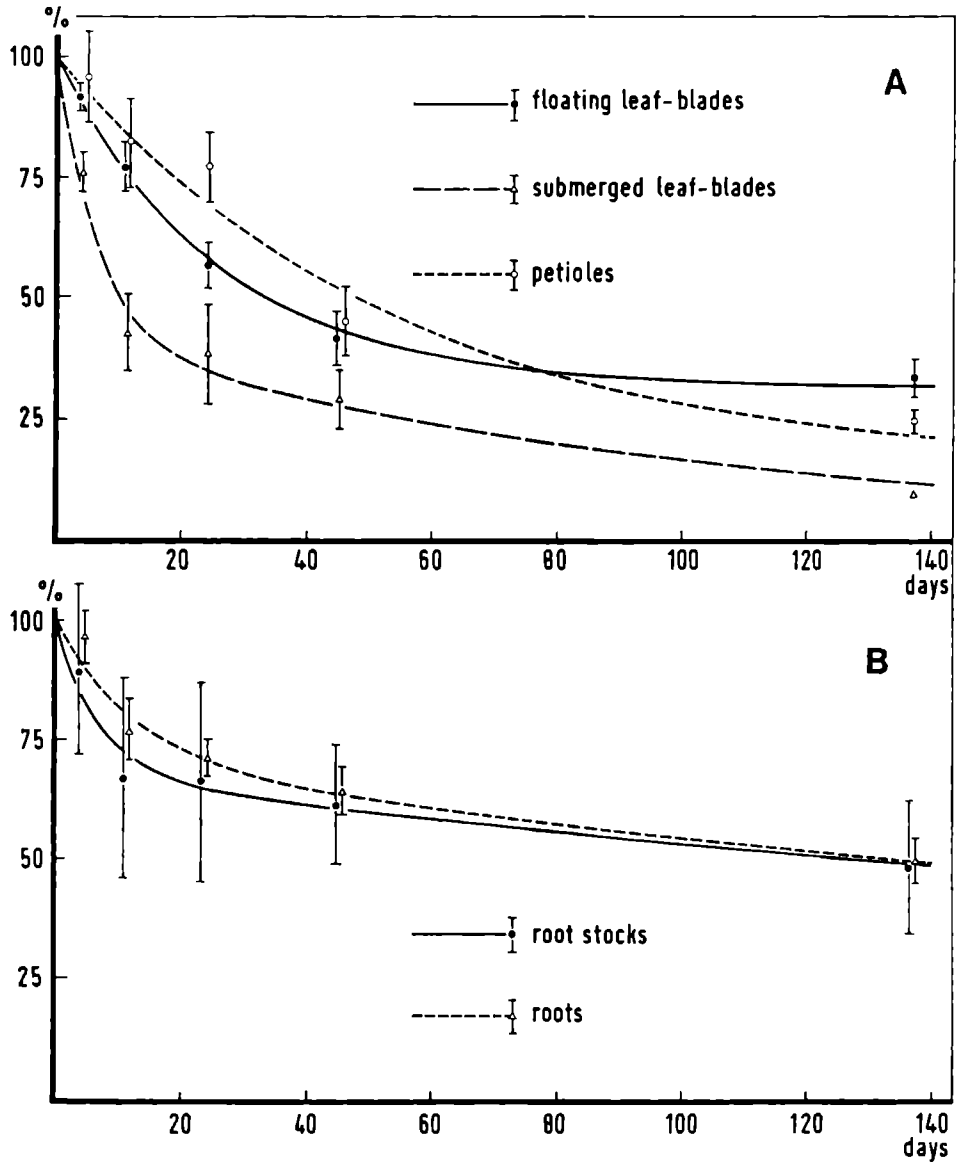

Fig. 2. Organic weight loss of decomposing aboveground (A) and underground (B) plant parts of *Nuphar lutea*. The dots and bars represent mean values of residual weight and standard deviations as actually measured. The lines represent the decomposition curves of the *Nuphar* material as determined by means of the "2-component model".

of the laminae of the submerged leaves was smaller than that of the other aboveground structures (Fig. 2; Table IA).

The decomposing floating leaves (leaf-blades) of *Nuphar lutea* in the Bemmelse Strang (autumn series) and the Oude Waal (summer series) show different breakdown patterns (Fig. 3A). These oxbow lakes in the vicinity of Nijmegen are nearly identical in hydrology and water chemistry. The recorded ranges in water temperature during the experiments in summer and autumn were 12—23°C and 2—18°C, respectively. Hence, the faster breakdown of the *Nuphar* leaves in summer can largely be explained by seasonal factors such as temperature. Although the quantity of the residual organic mass in the 0.78-mm bags was significantly smaller than that of the corresponding 0.27-mm bags on some sampling days (Table IB), the breakdown of the leaves in both types of litter bags showed very much the same pattern (Fig. 3A).

The breakdown of the *Nuphar* leaves in the Oude Waal, Grote Vilt and Voorste Choorven is presented in Fig. 3B. In the period of the decomposition experiment, there were considerable differences in trophic status of the water between these systems (Table II). The water from the Oude Waal was alkaline and fairly rich in nitrogen and phosphorus. In the same period, the water from the Grote Vilt had high concentrations of both nitrogen and phosphorus, while it also had extremely high pH and fairly low alkalinity values. The Voorste Choorven water had low pH and very low alkalinity values during the whole sampling period; furthermore, high nitrogen (particularly ammonium) and low phosphorus concentrations were found. During the decomposition experiment, the range in water temperature was more or less the same in the 3 systems (Table II). Although there were differences in the chemical properties of the Oude Waal

TABLE II

Physicochemical properties of the Oude Waal (O.W.), Grote Vilt (G.V.) and Voorste Choorven (V.Ch.) water during the decomposition experiments

	Site tested (July—October)		
	O.W.	G.V.	V.Ch.
Chemical composition (μmol l^{-1})			
Total N	45.6—59.6	81.0—150.7	86.5—152.9
NO_3^-/NO_2^-	0.7—1.8	0.2—4.6	1.2—4.0
NH_4^+	6.0—10.0	6.0—95.5	58.5—138.5
Total P	1.8—3.5	2.6—9.2	0.9—1.7
PO_4^{3-}	0.3—1.3	0.4—3.7	0.1—0.6
K^+	90—145	137—144	40—63
pH	7.2—8.2	8.6—9.1	4.0—4.4
Alkalinity meq l^{-1}	4.3—5.0	1.4—1.6	0.00—0.04
Temperature °C	12—23	12—24	11—24

and Grote Vilt medium, the decomposition patterns of the floating leaves were very similar in these 2 waters (Fig. 3B, Table IC). However, the amount of residual organic mass in the Voorste Choorven differed significantly

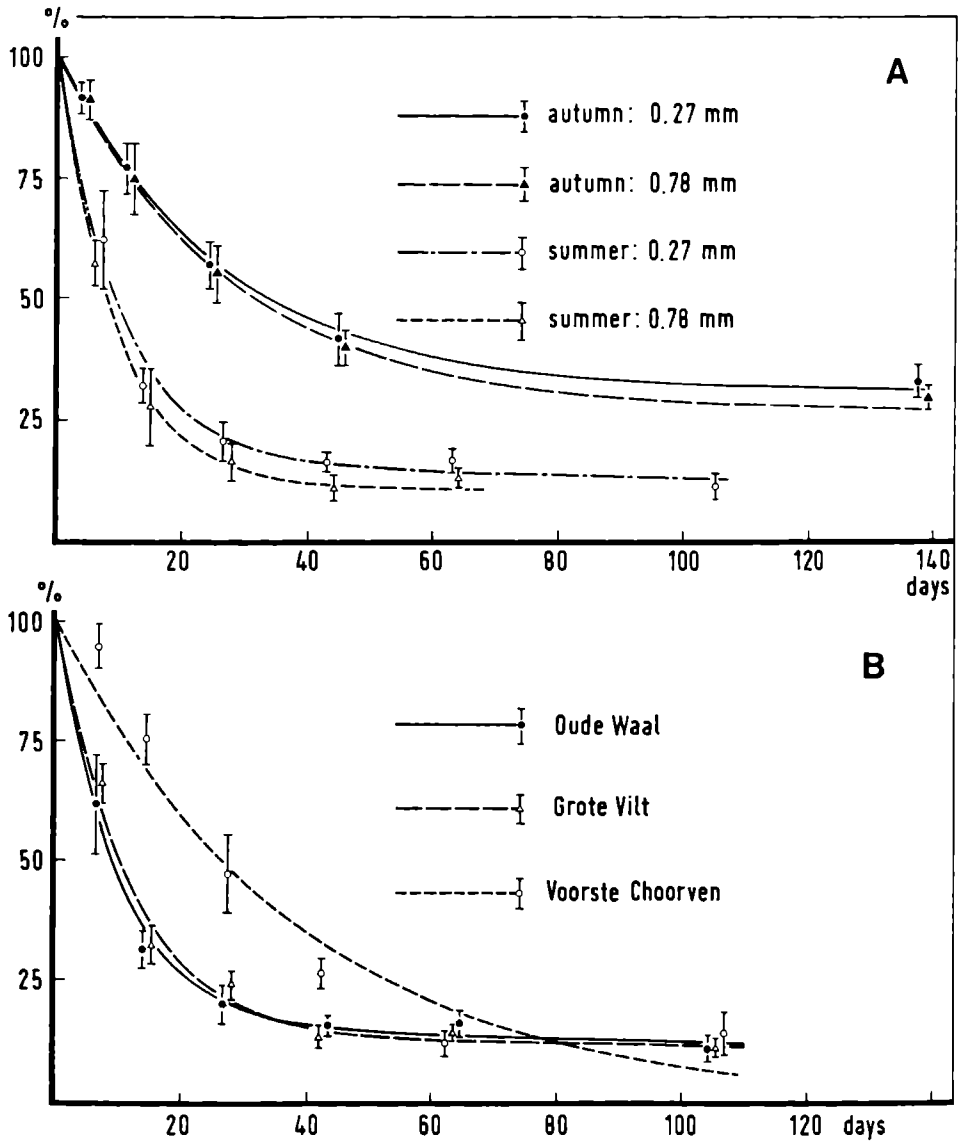

Fig. 3. The organic weight loss of decomposing laminae of *Nuphar lutea* floating leaves as influenced by the season and litter bag mesh size (A) and by the trophic status of the system (B). The dots and bars represent mean values of residual weight and standard deviations as actually measured. The lines represent the decomposition curves of the *Nuphar* material as determined by means of the "2-component model".

TABLE III

Breakdown parameters (k; a, b; R, KR, KL), their standard errors (s.e.) and coefficients of determination (C.D.) of the 3 mathematical models when fitted to the actual data of residual weight of decomposing *Nuphar lutea*

	Simple exponential model				Composite exponential models										
					Decaying coefficient model					Two-component model					
	n	Decay period (days)	k	s.e.	C.D.	a	s.e.	b	s.e.	C.D.	R	s.e.	KR	s.e.	KL	s.e.	C.D.
A. Floating leaves	30	137	0.0173	0.0018	0.7821	0.0310	0.0022	0.0263	0.0031	0.9644	0.3104	0.1335	0.0000	0.0032	0.0391	0.0097	0.9678
Submerged leaves	26	137	0.0489	0.0051	0.8035	0.0916	0.0117	0.0629	0.0136	0.9103	0.4178	0.0956	0.0097	0.0056	0.1596	0.0429	0.9349
Petioles	29	137	0.0138	0.0011	0.8985	0.0165	0.0020	0.0063	0.0035	0.9107	0.1427	1.6464	0.0000	0.0641	0.0186	0.0280	0.9126
Root-stocks	30	137	0.0087	0.0018	0.1624	0.0375	0.0150	0.0602	0.0318	0.4580	0.6695	0.1115	0.0023	0.0021	0.1433	0.1209	0.4764
Roots	29	137	0.0079	0.0009	0.6162	0.0203	0.0023	0.0298	0.0052	0.9021	0.7044	0.0549	0.0026	0.0008	0.0812	0.0273	0.9140
B. Autumn; 0.27 mm	30	137	0.0173	0.0018	0.7821	0.0310	0.0022	0.0263	0.0031	0.9644	0.3104	0.1335	0.0000	0.0032	0.0391	0.0097	0.9678
Autumn; 0.78 mm	30	137	0.0193	0.0017	0.8409	0.0310	0.0022	0.0228	0.0030	0.9631	0.2683	0.1702	0.0000	0.0049	0.0373	0.0105	0.9655
Summer; 0.27 mm	33	105	0.0659	0.0051	0.8987	0.0987	0.0077	0.0442	0.0065	0.9604	0.1568	0.0557	0.0021	0.0050	0.1000	0.0125	0.9637
Summer; 0.78 mm	30	63	0.0792	0.0051	0.9409	0.1065	0.0089	0.0402	0.0080	0.9663	0.1023	0.0806	0.0000	0.0154	0.1083	0.0159	0.9704
C. Oude Waal	33	105	0.0659	0.0051	0.8987	0.0958	0.0077	0.0442	0.0065	0.9604	0.1568	0.0557	0.0021	0.0050	0.1000	0.0125	0.9637
Grote Vilt	35	105	0.0599	0.0038	0.9273	0.0849	0.0050	0.0367	0.0043	0.9761	0.1321	0.0416	0.0009	0.0041	0.0860	0.0077	0.9797
Voorste Choorven	35	105	0.0264	0.0015	0.9428	0.0188	0.0026	−0.0199	0.0064	0.9467	0.0069	1.1119	0.0000	1.0976	0.0267	0.0200	0.9428

from that in the Oude Waal and Grote Vilt on 5 of the 6 sampling days (Table IC). The breakdown of the leaves was slower in this acid moorland pool, particularly during the initial decay period (Fig. 3B).

Comparison of the mathematical models

A higher coefficient of the determination (C.D. = r^2) corresponds with a better fit of the model to the decomposition data. Hence, the 2 composite exponential models describe the organic weight loss of the *Nuphar* material during its breakdown in the field better than the "simple exponential function". In most experiments, the "2-component model" showed a slightly better fit than the "decaying coefficient model" (Table III). However, the standard errors of the decay parameters of the "2-component model" were relatively high compared to those of the other functions (Table III). Furthermore, it appeared that the coefficients of determination were very low when the models were fitted to the decay data of the root-stocks (Table IIIA). This might be explained by the phenomenon that some incubated root-stocks in some litter bags persisted in a living state during the whole sampling period, while all other plant parts showed senescence and death within a short time.

TABLE IV

A statistical comparison (Student's *t*-test) of the breakdown parameters of each mathematical function as found for the different experiments and treatments[a]

	k	*a*	*b*	*R*	*KR*	*KL*
A. Floating leaves/submerged leaves	+	+	+	–	+	+
Floating leaves/petioles	+	+	+	–	–	–
Floating leaves/root-stocks	+	–	–	+	–	+
Floating leaves/roots	+	+	–	+	–	+
Submerged leaves/petioles	+	+	+	–	–	+
Submerged leaves/root-stocks	+	+	–	+	–	–
Submerged leaves/roots	+	+	+	+	–	+
Petioles/root-stocks	+	–	+	–	–	–
Petioles/roots	+	–	+	–	–	+
Root-stocks/roots	–	–	–	–	–	–
B. Autumn 0.27 mm/autumn 0.78 mm	–	–	–	–	–	–
Autumn 0.27 mm/summer 0.27 mm	+	+	+	–	–	+
Autumn 0.78 mm/summer 0.78 mm	+	+	+	–	–	+
Summer 0.27 mm/summer 0.78 mm	+	–	–	–	–	–
C. Oude Waal/Grote Vilt	–	–	–	–	–	–
Oude Waal/Voorste Choorven	+	+	+	–	–	+
Grote Vilt/Voorste Choorven	+	+	+	–	–	+

[a] +, Significantly different ($P < 0.05$); –, Not significantly different ($P > 0.05$).

The decay parameters, as determined for the decomposing *Nuphar* material with the 3 mathematical models, were statistically compared per parameter and per experiment (Table IV). In most cases, at least 1 parameter per model differed significantly when the breakdown rates of 2 plant parts of *Nuphar lutea* were compared. However, the decay parameters of all models as determined for the roots and root-stocks were not significantly different (Table IVA). When the results of the autumn and summer experiments are compared it is found that at least 1 parameter per mathematical model differed significantly, indicating a faster breakdown of the *Nuphar* leaves in summer. A significantly faster breakdown rate of the floating leaves in the 0.78-mm mesh bags than in the 0.27-mm mesh bags could only be demonstrated in summer, applying the "simple exponential model" (Table IVB). The decay parameters of the mathematical models used to describe the breakdown of *Nuphar* leaves in the 3 different aquatic systems showed a significant difference between the Voorste Choorven and the other systems, while those between the Oude Waal and Grote Vilt were nearly the same (Table IVC).

Nitrogen, phosphorus and potassium dynamics

In the present paper the patterns in nutrient dynamics of the decomposing *Nuphar* material are described in 2 different ways: qualitatively, as the changes in nutrient concentration of the detritus (right-hand sides of Figs. 4 and 5), quantitatively, as the changes in the relative nutrient stocks of the detritus present in the litter bags (left-hand sides of Figs. 4 and 5).

The initial nutrient content of the *Nuphar* material from the Bemmelse Strang depended on which part of the plant was being studied. In the same way the patterns of nitrogen, phosphorus and potassium dynamics of the decomposing *Nuphar* material differed for the different plant parts (Fig. 4). The nitrogen concentration of the detritus of all plant parts increased at least temporarily. The phosphorus and potassium concentrations of the detritus of most plant parts showed a net decrease with time or remained more or less at the same level. At the end of the decomposition experiment the detritus of most plant parts (except root-stocks) showed more or less similar nitrogen and potassium concentrations and atomic C/N ratios (Fig. 4). The relative stocks of nitrogen in the litter bags increased with time for the underground plant parts and decreased for the floating and submerged leaves. The relative amounts of phosphorus and potassium in the litter bags showed a net decrease with time for all plant parts (Fig. 4).

The initial nitrogen, phosphorus and potassium content of the floating leaf material was dependent on the system from which the plant material had been harvested. The patterns in nutrient dynamics of the decomposing leaves were also more or less site-dependent (Fig. 5). The nitrogen con-

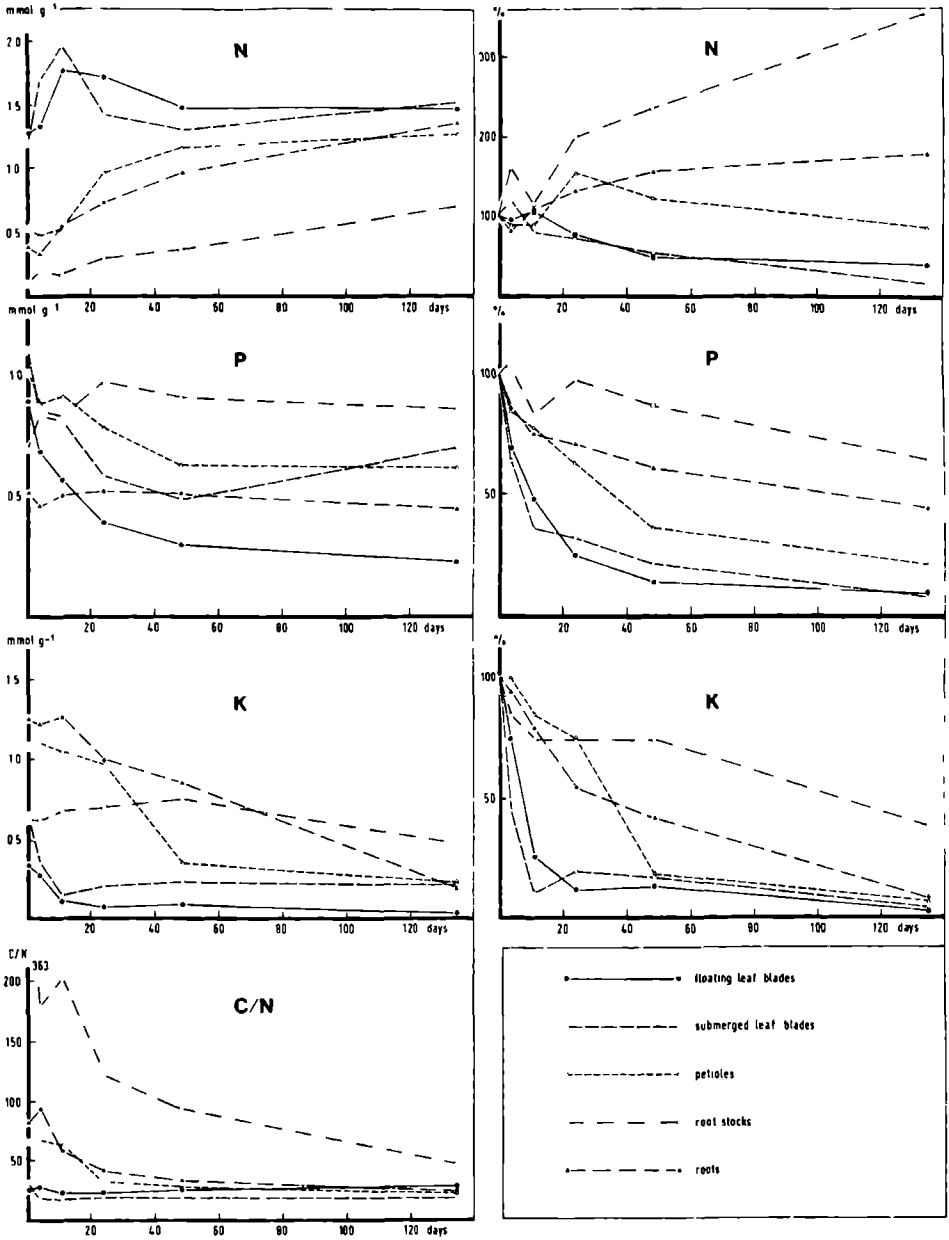

Fig. 4. Nitrogen, phosphorus, potassium and C/N ratio dynamics during breakdown of *Nuphar lutea* plant parts in the Bemmelse Strang, expressed as mmol g^{-1} dry weight (left) and as percentages of the original stock (right).

centration of the *Nuphar* detritus showed a temporary increase in all systems, although, this increase occurred at different times. A temporary increase in phosphorus concentration was observed in the *Nuphar* detritus from the Voorste Choorven and Grote Vilt. Nevertheless, the final nitrogen and phosphorus concentrations of the *Nuphar* detritus in the 3 systems were always lower than the initial concentrations. The potassium concentrations of the detritus steadily declined during the initial decay period in the 3 systems studied. In the course of the decomposition experiment the relative nitrogen and phosphorus concentrations of the leaf-detritus in the bags declined to less than 15% of the original levels in all systems,

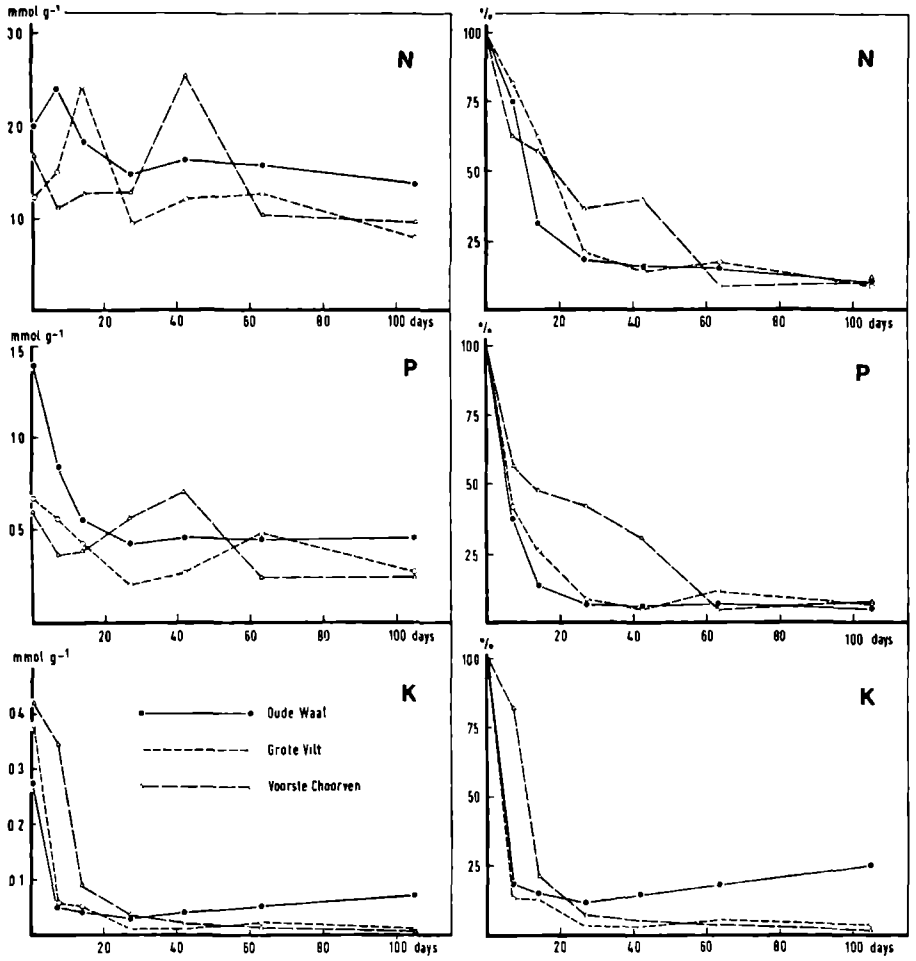

Fig. 5. Nitrogen, phosphorus and potassium dynamics during breakdown of the laminae of *Nuphar lutea* floating leaves in 3 systems which differ in trophic status, expressed as mmol g^{-1} dry weight (left) and as percentages of the original stock (right).

while the potassium concentration in the bags also declined during the initial decay period. However, later on a slight increase in potassium concentration was observed in the Oude Waal (Fig. 5).

DISCUSSION

In the present study, 3 mathematical models were used to describe the disappearance of the *Nuphar* detritus from the litter bags. It appeared that the in situ breakdown of the *Nuphar* detritus was described better by the composite exponential models than by the "simple exponential model". In most cases, the "2-component model" showed a slightly better description than the "decaying coefficient model". These findings are in agreement with the laboratory experiments presented by Carpenter (1982) and De Lyon et al. (1983). Although the application of the composite exponential models resulted in a better description of the breakdown of plant material, the single decay parameter of the "simple exponential model" is very convenient for comparative purposes (e.g., in a table) because the higher the parameter (k) the higher the overall breakdown. In the case of the composite exponential models the overall decay is more difficult to visualize when only the estimates of the decay parameters are given. In the present study, the standard errors of the parameters of the "2-component model" were very high when this model was fitted to the decay data of the petioles from the Bemmelse Strang (Table IIIA) and the leaves from the Voorste Choorven (Table IIIC). This phenomenon can be attributed to the fact that the decaying petioles from the Bemmelse Strang (Fig. 2A) and the decomposing leaves from the Voorste Choorven (Fig. 3B) did not show a gradual decrease in weight. The negative value for Parameter b of the "decaying coefficient model", when fitted to the decay data of the leaves from the Voorste Choorven (Table IIIC) can also be explained in this way. In the Voorste Choorven, decay started very slowly and increased later on when more cells became senescent, resulting in a very low value for Parameter a and consequently a negative value for Parameter b. In the mathematical models used, it is assumed that the decay of macrophyte material is a gradual process. However, in nature, decomposition usually starts with a lag phase. Furthermore, in the field, breakdown of plant material often is not a gradual process because of constantly changing environmental conditions (e.g. temperature). When applying the mathematical models, the problems caused by the occurrence of a distinct lag phase can only be overcome by excluding the initial observations and by choosing such a starting point that from there on the disappearance of decomposing material is a more or less gradual process. Furthermore, it can be argued that more sampling days are required if the decay parameters of the composite exponential models are used for comparative purposes. Carpenter (1982) and De Lyon et al. (1983) also illustrated that care must be taken in interpreting the individual estimates of the

parameters in terms of overall decay, particularly when the number of measurements is small and the number of parameters per model is larger. Therefore, when mathematical models are used to describe the breakdown of macrophytes it is advisable to give not only the decay parameters and/or the predicted breakdown curves but also the actual data of residual weight.

Despite the common occurrence of *Nuphar lutea* in freshwater ecosystems in Europe very little information on the decomposition of this species is available. The present study on *Nuphar lutea* as well as investigations on *Nuphar variegatum* Engelm. (Godshalk and Wetzel, 1978) and *Nuphar advena* Ait. (Twilley, 1976; Odum and Heywood, 1978), indicate a relatively fast decomposition rate of members of the genus *Nuphar* as compared to several submerged and emergent aquatic macrophytes. The decomposability of plant material is a function of the relative proportion of labile and refractory components in the detritus. The protoplasmic component of plant material will be rapidly lost during breakdown, whereas cell walls are more persistent due to the relatively high amounts of cellulose, hemicellulose and lignin. According to Esteves (1979) *Nuphar lutea* has a relatively small cell-wall fraction as compared to several submerged and emergent water plants. A relatively small initial fiber content is also recorded for *Nuphar variegatum* by Godshalk and Wetzel (1978). Boon and Haverkamp (1982) reported relatively low amounts of lignin in green leaves of *Nuphar variegatum* while prolonged decomposition of this material resulted in residues with an increased lignin content. Hence, the relatively fast breakdown of *Nuphar* can be explained in part by its relatively low content in structural carbohydrates.

In the present study, it was found that some plant parts of *Nuphar lutea* showed significant differences in breakdown rate. Different decay rates for different morphological structures are mentioned for several emergent (Hackney and De la Cruz, 1980; Blake, 1982; Sharma and Gopal, 1982; Howard-Williams et al., 1983), floating-leaved (Esteves and Barbieri, 1983; Brock, 1984; this study) and submerged (Bastardo, 1979) macrophytes. In this respect, it is worth mentioning that the various organs of macrophytes may also produce different amounts of organic matter. The annual biomass production of *Nuphar lutea* is largely produced by the aboveground plant parts, whereas sometimes this species has more than 80% of its peak biomass underground due to many years of biomass accumulation. The roots and root-stocks of *Nuphar lutea* both have a longer life span and a slower breakdown than the aboveground plant parts. Under natural circumstances the senescence of root-stocks is a very slow process. In the present study some incubated root-stocks in some litter bags persisted in a living state during the entire sampling period. Apparently the physiological condition of the root-stock material used was not the same, which makes it difficult to interpret the decay data of the root-stocks. Nevertheless, it may be argued that the slower breakdown of roots and

root-stocks can be explained in part by their low initial nitrogen levels. According to Godshalk and Wetzel (1978) decay rates of macrophyte material are not only related to initial fiber contents, but also to initial nitrogen levels, in such a way that tissues with low nitrogen and high fiber levels have the lowest decomposition rate. However, besides the chemical composition of the roots and root stocks of *Nuphar lutea*, the anoxic conditions in the sediment may also have slowed down the decomposition of the underground organs in the present study. When examining the in vitro decay data of *Nuphar lutea* as presented by De Lyon et al. (1983) it appears that this species has a slower breakdown under anaerobic than under oxygen-rich conditions. Furthermore, differences in shape between the various organs of *Nuphar* and differences in nutrient level between the hydrosoil and the overlying water might also cause variations in decomposability, at least in the initial phase. The faster breakdown of the laminae of the submerged leaves of *Nuphar* as compared to that of the laminae of the floating leaves is probably caused by the larger surface area to volume ratio of the submerged leaf-blades. In general it can be concluded that the observed differences in patterns of weight loss of various *Nuphar* plant parts can largely be explained by: differences in chemical composition and amounts of structural carbohydrates between morphological structures; differences in surface area to volume ratio between plant parts; differences in location within the water-sediment column between plant parts and associated physico-chemical conditions and decomposers.

It is shown in the present paper that the disappearance of the decomposing *Nuphar lutea* leaves from the litter bags is influenced by seasonal factors. The breakdown of the coarse detritus was significantly faster in summer than in autumn. It seems likely that this phenomenon is for the greater part caused by the higher temperatures in summer. However, seasonal differences in the physiological state of the plant material might also be of importance. The initial nitrogen content of the *Nuphar* leaves, which were used in the summer experiment was much higher than that of the leaves incubated in autumn. Both temperature and initial nitrogen content have been shown experimentally to influence weight-loss during breakdown of macrophytes (Godshalk and Wetzel, 1978; Carpenter and Adams, 1979). Furthermore, the higher temperatures in summer with certainty stimulated the activities of the detritivores in the litter bags. In summer up to 530 macro-invertebrate individuals were found per g AFDW of *Nuphar* detritus, whereas in autumn the maximum number of macro-invertebrate individuals was only 58 per g AFDW (Th.C.M. Brock, unpublished results). It seems likely that the observed differences in the breakdown rate of *Nuphar* leaves between the litter bags with a 0.27 and 0.78 mm mesh size is partly caused by the macro-fauna, although the loss of larger particles from the larger mesg-bags also plays a part in this.

It was found in the present study that the patterns of organic weight

loss and/or nutrient dynamics of the decomposing *Nuphar lutea* leaves varied between the Oude Waal, Grote Vilt and Voorste Choorven. During the experiment the ranges in water temperature in the systems studied were more or less the same, so that the observed differences can largely be explained by: differences in the chemical composition of the *Nuphar* material itself (see e.g., Fig. 5); differences in chemical composition of the medium between the systems (Table II).

Several investigators have indicated a faster breakdown rate of plant material when the medium is enriched with nitrogen (e.g., Howarth and Fisher, 1976; Carpenter and Adams, 1979) or with a combination of nitrogen and phosphorus (e.g., Howarth and Fisher, 1976; Polunin, 1982). Furthermore, the decomposition data presented by Carpenter and Adams (1979) indicate that the difference in decay between an experiment using plant material with a high nitrogen content and without N-enrichment of the medium and an experiment using the same type of plant material low in nitrogen and with N-enrichment of the medium, was not significant. Hence, the more or less similar pattern of organic weight loss of *Nuphar* leaves in the Oude Waal and Grote Vilt might be explained in this way; in the Grote Vilt the nitrogen and phosphorus levels were relatively low in the *Nuphar* tissues and relatively high in the water, whereas in the Oude Waal the reverse was the case. The slower breakdown of *Nuphar* leaves in the Voorste Choorven can largely be explained by the low pH and low alkalinity values of the water. A slower decomposition of plant material in acid environments is also reported by Grahn et al. (1974), McKinley and Vestal (1982) and Carpenter et al. (1983).

In the present study, the patterns of nitrogen, phosphorus and potassium dynamics of the decomposing *Nuphar* material were dependent on the type of plant part, the season and the system. The observed differences in nutrient dynamics between plant parts are influenced by the way the nutrients are incorporated in the labile or refractory component of the detritus, by differences in initial nutrient content and by the location of the plant parts within the water-sediment column. In all experiments of the present study, the *Nuphar* detritus showed at least a temporary increase in nitrogen concentration. An increase in the nitrogen concentration in macrophyte detritus is frequently reported in literature and is often attributed to microbial biomass. However, Iversen (1973) and Andersen (1978) estimated that microbial biomass was insufficient to account for the total nitrogen increase in plant detritus. An increase in the concentration of a certain element in macrophyte detritus might be attributed to several factors such as the association of the element with the refractory component of the detritus, adsorption processes (Howard-Williams and Davies, 1979), contamination with sediment material and dead parts of invertebrates (Brock, 1984), a high nutrient concentration in the microbial biomass (Fenchel, 1970) and/or extracellular excretions of micro-organisms associated with the detritus (Hobbie and Lee, 1980;

Robinson et al., 1982) and complex biochemical processes such as humification (Godshalk and Wetzel, 1978).

It is evident that in the field numerous factors influence the decay and nutrient dynamics of macrophyte detritus. Nevertheless, some factors will be more important than others. Laboratory experiments and detailed chemical analyses of the detritus will be required to reveal the effects of the individual environmental parameters, as well as combinations of them, on the decomposition of macrophytes. This knowledge is important for the assessment of the impact of eutrophication and acidification on the decomposition of plant material and the cycling of organic matter and nutrients in aquatic ecosystems.

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REFERENCES

Andersen, F.Ø., 1978. Effects of nutrient level on the decomposition of *Phragmites communis* Trin. Arch. Hydrobiol., 84: 42—54.

Bastardo, H., 1979. Laboratory studies on the decomposition of littoral plants. Pol. Arch. Hydrobiol., 26: 267—299.

Blake, G., 1982. Characterization of decomposition of plant material in an alpine lake. Hydrobiol. Bull. (Amsterdam), 16: 5—9.

Boon, J.J. and Haverkamp, J., 1982. Pyrolysis mass spectrometry of intact and decomposed leaves of *Nuphar variegatum* and *Zostera marina*, and some archeological eelgrass samples. Hydrobiol. Bull. (Amsterdam), 16: 71—82.

Brock, Th.C.M., 1984. Aspects of the decomposition of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Aquat. Bot., 19: 131—156.

Brock, Th.C.M. and Van der Velde, G., 1983. An autecological study on *Hydromyza livens* (Fabricius) (Diptera, Scatomyzidae), a fly associated with nymphaeid vegetation dominated by *Nuphar*. Tijdschr. Entomol., 126: 59—90.

Brock, Th.C.M., Huijbrechts, C.A.M., Van der Steeg-Huberts, M.J.H.A. and Vlassak, M.A., 1982. In situ studies on the breakdown of *Nymphaoides peltata* (Gmel.) O. Kuntze (Menyanthaceae); some methodological aspects of the litter bag technique. Hydrobiol. Bull. (Amsterdam), 16: 35—49.

Brock, Th.C.M., Bongaerts, M.C.M., Heijnen, G.J.M.A. and Heijthuijsen, J.H.F.G., 1983. Nitrogen and phosphorus accumulation and cycling by *Nymphoides peltata* Gmel.) O.Kuntze (Menyanthaceae). Aquat. Bot., 17: 189—214.

Carpenter, J., Odum, W.E. and Mills, A., 1983. Leaf litter decomposition in a reservoir affected by acid mine drainage. Oikos, 41: 165—172.

Carpenter, S.R., 1982. Comparisons of equations for decay of leaf litter in tree-hole ecosystems. Oikos, 39: 17—22.

Carpenter, S.R. and Adams, M.S., 1979. Effects of nutrients and temperature on decomposition of *Myriophyllum spicatum* L. in a hard water eutrophic lake. Limnol. Oceanogr., 24: 520—528.

Delbecque, E.J.P., 1983. A comparison of the periphyton of *Nuphar lutea* and *Nymphaea alba*. In: R.G. Wetzel (Editor), Periphyton of Freshwater Ecosystems. Developments in Hydrobiology, 17: 41—47.

Delbecque, E.J.P. and Chatrou, A.H.C., 1983. A comparison of the periphyton of *Nuphar lutea* and *Nymphaea alba*. The distribution of multicellular algae and *Vorticella* spp. on the undersides of floating leaves. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18—23 September 1983, pp. 57—62.

De Lyon, M.J.H., Van Laar, E.M.J.M. and Brock, Th.C.M., 1983. A comparison of three mathematical models for the description of breakdown of *Nuphar lutea* detritus. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18—23 September 1983, pp. 129—133.

Den Hartog, C., 1978. Structural and functional aspects of macrophyte-dominated systems. Proc. EWRS 5th Symp. Aquat. Weeds, pp. 35—41.

Den Hartog, C., 1983. A short survey of the research topics of the Laboratory of Aquatic Ecology, Catholic University, Nijmegen, including a literature list. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18—23 September 1983, pp. 1—15.

Esteves, F.A., 1979. Die Bedeutung der aquatischen Makrophyten für den Stoffhaushalt des Schöhsees. II. Die organischen Hauptbestandteile und der Energiegehalt der aquatischen Makrophyten. Arch. Hydrobiol., 57: 144—187.

Esteves, F.A. and Barbieri, R., 1983. Dry weight and chemical changes during decomposition of tropical macrophytes in Lobo Reservoir, Saõ Paulo, Brazil. Aquat. Bot., 16: 285—295.

Fenchel, T.M., 1970. Studies on the decomposition of organic detritus derived from the turtle grass *Thalassia testudinum*. Limnol. Oceanogr., 15: 14—20.

Giesen, Th.G. and Van der Velde, G., 1983. Ultraviolet reflectance and absorption patterns in flowers of *Nymphaea alba* L., *Nymphaea candida* Presl and *Nuphar lutea* (L.)Sm. (Nymphaeaceae). Aquat. Bot., 16: 369—376.

Godshalk, G.L. and Wetzel, R.G., 1978. Decomposition of aquatic angiosperms. II. Particulate components. Aquat. Bot., 5: 301—327.

Goodnight, J.H., 1979. NLIN procedure. In: SAS User's Guide, 1979 edn. SAS Institute, Cary, NC, pp. 315—329.

Grahn, O., Hultberg, H. and Landner, L., 1974. Oligotrophication — a self-accelerating process in lakes subjected to excessive supply of acid substances. Ambio, 3: 93—94.

Hackney, C.T. and De la Cruz, A.A., 1980. In situ decomposition of roots and rhizomes of two tidal marsh plants. Ecology, 61: 226—231.

Hobbie, J.E. and Lee, C., 1980. Microbial production of extracellular material: importance in benthic ecology. In: K.R. Tenore and B.C. Coull (Editors), Marine Benthic Dynamics. University of South Carolina Press, Columbia, pp. 341—346.

Howard-Williams, C. and Davies, B.R., 1979. The rates of dry matter and nutrient loss from decomposing *Potamogeton pectinatus* in a brackish south-temperate coastal lake. Freshwater Biol., 9: 13—21.

Howard-Williams, C., Pickmere, S. and Davies, J., 1983. Decay rates and nitrogen dynamics of decomposing watercress (*Nasturtium officinale* R.Br.). Hydrobiologia, 99: 207—214.

Howarth, R.W. and Fisher, S.G., 1976. Carbon, nitrogen, and phosphorus dynamics during leaf decay in nutrient enriched stream micro-ecosystems. Freshwater Biol., 6: 221—228.

Iversen, T.M., 1973. Decomposition of autumn-shed beech leaves in a spring-brook and its significance for the fauna. Arch. Hydrobiol., 72: 305—312.

Jenny, H., Gessel, S.P. and Bingham, F.T., 1949. Comparative study of decomposition of organic matter in temperate and tropical regions. Soil Sci., 68: 419—432.

Larsen, V.J., 1982. The effect of pre-drying and fragmentation on the leaching of nutrient elements and organic matter from *Phragmites australis* (Cav.) Trin. litter. Aquat. Bot., 14: 29—39.

Lousier, J.D. and Parkinson, D., 1976. Litter decomposition in a cool temperate deciduous forest. Can. J. Bot., 54: 419—436.

McKinley, V.L. and Vestal, J.R., 1982. Effects of acid on plant litter decomposition in an arctic lake. Appl. Environ. Microbiol., 43: 1188—1195.

Odum, W.E. and Heywood, M.A., 1978. Decomposition of intertidal freshwater marsh plants. In: R.E. Good, D.F. Whigham and R.L. Simpson (Editors), Freshwater Wetlands. Academic Press, New York, pp. 89—97.

Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology, 44: 322—331.

Polunin, N.V.C., 1982. Processes contributing to the decay of reed (*Phragmites australis*) litter in fresh water. Arch. Hydrobiol., 94: 192—209.

Robinson, J.D., Mann, K.H. and Novitsky, J.A., 1982. Conversion of the particulate fraction of seaweed detritus to bacterial biomass. Limnol. Oceanogr., 27: 1072—1079.

Rogers, K.H. and Breen, C.M., 1982. Decomposition of *Potamogeton crispus* L.: the effect of drying on the pattern of mass and nutrient loss. Aquat. Bot., 12: 1—12.

Roijackers, R.M.M., 1983. Primary productivity of the phytoplankton in the Oude Waal near Nijmegen, The Netherlands. A comparison between the nymphaeid dominated zone and the open water zone. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18—23 September 1983: pp. 203—207.

Roijackers, R.M.M., 1984. Some structural characteristics of the phytoplankton in the Oude Waal near Nijmegen, The Netherlands. XXIInd SIL-congress, Lyon, France, 21—28 August 1983, in press.

Scheffé, H., 1959. The Analysis of Variance. A Wiley Publication in Mathematical Statistics. John Wiley, New York, 477 pp.

Sharma, K.P. and Gopal, B., 1982. Decomposition and nutrient dynamics in *Typha elephantina* Roxb. under different water regimes. In: B. Gopal, R.E. Turner, R.G. Wetzel and D.F. Whigham (Editors), Wetlands: Ecology and Management. Int. Sci. Publs., Jaipur, pp. 321—335.

Twilley, R.R., 1976. Phosphorus cycling in *Nuphar* communities. In: M.M. Brinson and G.J. Davies (Editors), Primary productivity and mineral cycling in aquatic macrophyte communities of the Chowan River, North Carolina. Water Resources Research Institute, University of North Carolina, Report No. 120, 173 pp.

Van der Velde, G., 1978. Structure and function of a nymphaeid-dominated system. Proc. EWRS 5th Symp. Aquat. Weeds, pp. 127—133.

Van der Velde, G., 1980. Studies in nymphaeid-dominated systems with special emphasis on those dominated by *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Thesis, Catholic University Nijmegen, Stichting Studentenpers Nijmegen, The Netherlands, 163 pp.

Van der Velde, G. and Peelen-Bexkens, P.M.M., 1983. Production and biomass of floating leaves of three species of Nymphaeaceae in two Dutch waters. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18—23 September 1983, pp. 230—235.

Wieder, R.K. and Lang, G.E., 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology, 63: 1636—1642.

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THE EFFECTS OF THE SEASON AND OF WATER CHEMISTRY ON THE DECOMPOSITION OF *NYMPHAEA ALBA* L.; WEIGHT LOSS AND PYROLYSIS MASS SPECTROMETRY OF THE PARTICULATE MATTER

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ABSTRACT

Brock, T.C.M., Boon, J.J. and Paffen, B.G.P., 1985. The effects of the season and of water chemistry on the decomposition of *Nymphaea alba* L.; Weight loss and pyrolysis mass spectrometry of the particulate matter. *Aquat. Bot.*, 22: 197—229.

Dynamics in loss of mass and changes in organic matter composition of decomposing leaves of *Nymphaea alba* L. were studied in the ambient water of an alkaline eutrophic oxbow lake and an acid moorland pool. These aspects were also studied in the laboratory, in open flow-through aquaria fed with media differing in pH, alkalinity and nitrogen and/or phosphorus concentrations. The loss in weight of the decomposing leaves was studied using litter bags. The organic matter composition of the particulate residues was characterized by Curie-point pyrolysis mass spectrometry.

Higher weight-loss rates and faster changes in organic matter composition were observed in the warmer period of the year and under more eutrophic and/or alkaline conditions. In acid environments, the loss of structural carbohydrates from the decomposing plant material was small. In eutrophic and/or alkaline environments, lignin accumulated in the particulate residues, while cellulose and hemicellulose were apparently mineralized.

INTRODUCTION

In many relatively small and shallow freshwater ecosystems in The Netherlands, aquatic vascular plants are a common feature. Here, they frequently play an important role in organic matter production and as an energy source for other organisms. In general, only a relatively small proportion of the production of aquatic macrophytes is grazed by herbivores, so that most of the plant material produced senesces and undergoes decomposition. Usually, a large proportion of the decomposing plant material is metabolised by microorganisms, which, in their turn, are an excellent food for detritivores.

Microbial activity, and thus the rate of decomposition of aquatic macrophytes, is influenced by the physico-chemical properties of the water. Within a lake, seasonal changes in several physico-chemical factors can be observed. There also exists a large variation in the trophic status of aquatic ecosystems in which macrophytes occur. Furthermore, during the past three decades, the chemical properties of many waters in The Netherlands have changed in a complex way due to eutrophication, alkalinisation or acidification (e.g., Roelofs, 1983). Both field and laboratory studies are required to reveal the effects of these complex processes and of individual chemical parameters on the decomposition of macrophyte material.

Most decomposition studies on aquatic macrophytes determine the changes in mass of the particulate organic matter, without describing detailed chemical changes in the detritus. However, from an ecological and biogeochemical point of view, this information is very important. Recently, analytical techniques have been developed for the characterisation of organic matter at the molecular level which employ Curie-point pyrolysis mass spectrometry (Meuzelaar et al., 1982). In this method, the plant material is depolymerised by thermal energy (Curie-point pyrolysis) and the evolved pyrolysis products are analysed on-line by mass spectrometry. Quantitative data on changes in organic matter composition in a series of samples can be obtained by factor-discriminant analysis of the mass spectral "finger prints" (Windig et al., 1983). These data provide some understanding of the changes in organic matter composition, for example during the process of plant material decay. Both living and time-resolved series of decaying macrophyte material have been analysed (Boon and Haverkamp, 1982; Boon et al., 1982, 1983a, b).

The present paper deals with aspects of the decomposition of *Nymphaea alba* L. This floating-leaved macrophyte was studied in the project on the structure and functioning of nymphaeid-dominated systems (Van der Velde, 1980; Van der Velde and Peelen-Bexkens, 1983). In The Netherlands, *Nymphaea alba* can be found in fresh waters which differ considerably in trophic status; furthermore, this species keeps its ground fairly well in eutrophicated and acidified aquatic ecosystems.

The objectives of the present paper are to describe the dynamics in loss of mass and changes in the major structural components of decomposing *Nymphaea alba* leaves under the following conditions: (1) in the field, in the ambient water of 2 systems which differ in trophic status and pH; and (b) in the laboratory, under defined environmental conditions in water which differs in pH, alkalinity and nutrient level.

MATERIALS AND METHODS

The field experiments

In the present study, the litter bag (mesh bag) technique, as described

by Brock et al. (1985), was used to study the in situ decomposition of *Nymphaea alba*. Polyethylene litter bags (35 × 35 cm) with a 0.27-mm mesh size were employed. Litter bags with laminae of floating leaves were incubated in the Oude Waal and in the Voorste Choorven. The Oude Waal is an alkaline eutrophic oxbow lake in the vicinity of Nijmegen (Province of Gelderland) and the Voorste Choorven is an acidified moorland pool near Oisterwijk (Province of Noord-Brabant). The *Nymphaea* material used in the experiments was harvested in the Oude Waal and Voorste Choorven and returned to each system in litter bags within 48 h. The harvested leaves were washed, placed for a few seconds between filter paper to remove adherent water and weighed in packets of approximately 10 leaves. Each packet was enclosed in a litter bag. Between these procedures, the leaves were stored at 4°C in the dark. Fresh material was used in the decomposition experiments because pre-drying of plant material affects weight loss and nutrient release (Brock et al., 1982; Rogers and Breen, 1982). The summer experiment started on 6 July 1982 and after 0, 7, 14, 28, 42, 62 and 105 days of incubation, 5 bags with decaying leaves were retrieved from the Oude Waal. Litter bags from the summer experiment in the Voorste Choorven could only be retrieved after 0, 7 and 14 days of incubation; the other bags were lost due to vandalism. The autumn experiment started on 21 September 1982 and after 0, 7, 14, 28, 49, 70 and 105 days of incubation, 5 bags were again retrieved from the Oude Waal and Voorste Choorven. On each sampling day, water samples of the Oude Waal and Voorste Choorven were also collected for physico-chemical analyses. Nutrient analyses were performed according to the methods described in Brock et al. (1983) and Roelofs (1983).

In the summer of 1982, a transplantation experiment was performed to study the effect of the origin of the plant material on weight loss during decomposition. *Nymphaea* leaves from both the Oude Waal and Voorste Choorven were placed separately in litter bags as described above and incubated in the water of an outdoor concrete tank (length 200 cm, width 135 cm, depth 80 cm) in the grounds of the university. After 0, 7, 14, 21, 28 and 34 days, 5 litter bags from each series were retrieved from the concrete tank.

At the end of each decay period in the Oude Waal, Voorste Choorven, and concrete tank, the residual plant material of each bag was dried (24 h; 105°C) and ground until visual sample homogeneity was obtained. Subsamples of the detritus were ashed (4 h; 550°C) in a muffle furnace to determine the ash-free dry weight (AFDW). In the field experiments, the AFDW of the detritus was always determined because of possible contamination of the decomposing plant material with sediment particles. The relative amount of residual mass in each incubated and retrieved bag was calculated as described by Brock et al. (1985). The values of residual weight obtained for the different treatments were compared statistically per sampling day by applying the one-way analysis of variance and Scheffé's simul-

taneous test (Scheffé, 1959). An exponential function was fitted to the data of residual weight of each treatment. The exponential function used is of the type, $W_t = W_0 \cdot \exp(-kt)$, which is the solution of $dW/dt = -kW$, where W_t is the mass remaining after a time interval t (in the present paper measured in days), W_0 the initial mass, exp the base of the natural logarithm, and k is the rate constant (cf. Jenny et al., 1949; Olson, 1963). The breakdown rates obtained with the above-mentioned function for the different treatments were statistically compared by means of the Student's t-test.

The laboratory experiments

The *Nymphaea* leaves which were used in the laboratory experiments were collected in the Oude Waal (Experiment I) or in the Voorste Choorven (Experiments II, III and IV). Experiment I started on 21 July and Experiments II, III and IV on 10 September, 15 October and 9 November, respectively. Polyethylene litter bags (18 × 18 cm) with a 0.25-mm mesh size were employed. From the harvested and cleaned leaves of *Nymphaea*, leaf discs with a diameter of 25 mm were obtained, avoiding the midrib area. In each litter bag a random selection of 30 leaf discs was enclosed, the total of which was precisely weighed. The decomposition experiments were conducted in glass aquaria (length 25 cm, width 25 cm and height 31 cm) which were placed in a stainless steel waterbath (Fig. 1). The temperature of the waterbath was maintained at 20°C. The water in the glass aquaria was continuously refreshed (1 l h^{-1}) from black polyethylene 120-l stock containers by means of peristaltic pumps. All laboratory experiments were performed in the dark to prevent photosynthetic production. Several series of litter bags with leaf discs were incubated in the various glass aquaria,

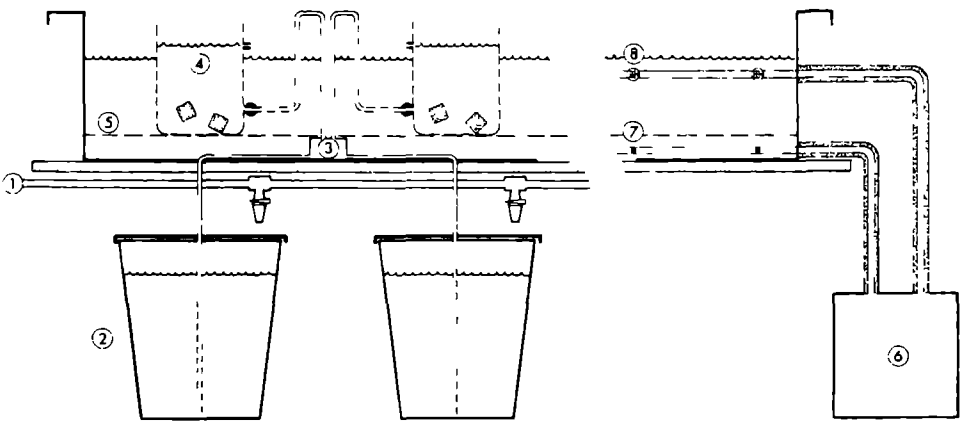

Fig. 1. Experimental set-up for the laboratory decomposition experiments. (1) demi-water supply; (2) polyethylene stock containers; (3) peristaltic pumps; (4) glass aquaria with litter bags; (5) waterbath; (6) cooling and heating aggregate; (7) inflow; (8) outflow.

TABLE I

Chemicals added to 100 l twice-demineralized water; the medium thus obtained was used as a basic medium (control medium)

5.00 g synthetic sea salt (Wimex, Wiegandt GMBH & Co., Krefeld)
1.70 g $CaSO_4.2H_2O$
2.93 g NaCl
0.15 g KCl
0.04 g Fe (III) NaChelate
0.01 mg $CuSO_4.5H_2O$
7.50 mg $MnCl_2(H_2O)$
1.00 mg $ZnSO_4.7H_2O$
0.10 mg $(NH_4)_6Mo_7O_{24}$
0.25 mg $CoCl_2.6H_2O$
0.25 mg H_3BO_3
0.25 mg NH_4VO_3

TABLE II

The various treatments used in the different laboratory experiments (I—IV); the nutrients mentioned were added to the control medium. The treatments from which samples were chosen for pyrolysis are indicated with an asterix

Treatments		Experiment			
		I	II	III	IV
Control medium		+	+	*	*
HCO_3^-	500 μmol l^{-1}	+	+		
HCO_3^-	1000 μmol l^{-1}	+	+		
HCO_3^-	5000 μmol l^{-1}	+	+	+	
NO_3^-	10 μmol l^{-1}	+	+		
NO_3^-	100 μmol l^{-1}	+	+	*	
NH_4^+	10 μmol l^{-1}	+			
NH_4^+	100 μmol l^{-1}	+			
PO_4^{3-}	0.5 μmol l^{-1}	+	+		
PO_4^{3-}	5.0 μmol l^{-1}	+	+	+	
pH 3	(HCl)			*	*
pH 8	(NaOH)			*	*
NO_3^-	100 μmol l^{-1} + PO_4^{3-} 5.0 μmol l^{-1}			*	
NO_3^-	100 μmol l^{-1} + HCO_3^- 5000 μmol l^{-1}			+	

which contained water with a different nutrient concentration. The principal medium (control medium) used in all laboratory experiments was composed synthetically, analogous to Roelofs et al. (1984), by adding certain chemicals to twice-demineralized water (see Table I). In some laboratory experiments, ammonium or nitrate were added to the control medium

in the form of NH_4Cl and KNO_3, in others, phosphate and bicarbonate as NaH_2PO_4 and $NaHCO_3$. In other treatments HCl and/or NaOH solutions were added (daily) to the principal medium to obtain (and maintain) water with pH values of approximately 3 and 8. The various media which were employed to study the in vitro decay of *Nymphaea alba* are presented in Table II. The nutrient concentrations and the pH of the applied media were chosen within the range in which *Nymphaea alba* is normally found in The Netherlands. In the laboratory experiments, 4 litter bags with decomposing leaf material were retrieved from the various media after 0, 7, 14, 21 and 28 days. The residual plant material of each bag was dried (24 h; 105°C) and weighed. The values of residual weight thus obtained were statistically compared and fitted to an exponential function as described above.

Organic matter analyses

Sample choice and pretreatment

A number of field and laboratory samples was chosen for pyrolysis. From the field experiments, the Oude Waal summer (6 July 1982), Oude Waal autumn (21 September 1982) and the Voorste Choorven autumn (21 September 1982) sample series were chosen. From the laboratory samples, the complete reference series of the Laboratory III and Laboratory IV experiments were analysed, whereas only particulate residues after 28 days of decomposition were chosen from selected treatments. Samples were chosen from the treatment with pH 3 and pH 8 for both Laboratory III and Laboratory IV material. Furthermore, from Laboratory III material, the residues from the treatments with added bicarbonate and the one with added nitrate and orthophosphate were also selected (see also Table II). Homogenised oven-dried plant material was available for analysis. This material was ground to a fine powder in glass mortars and about 1 mg of each sample was suspended in methanol by ultrasonication. Aliquots of 10 μl of this suspension were placed on ferromagnetic sample wires and the solvent was removed in vacuo. These sample carriers were placed in glass liners and analysed within 1 h in the pyrolysis mass spectrometer.

Curie-point pyrolysis mass spectrometry

The Curie-point pyrolysis mass spectra were obtained with an instrument made in the FOM-Institute for Atomic and Molecular Physics (Amsterdam), equipped with an automatic sampling exchange system, a Curie-point pyrolysis unit, a heated expansion volume and inlet system, a liquid nitrogen-cooled ion chamber, a quadrupole mass analyser (Balzers QMA 150/QMG 511) and an ion-counting detection system (Meuzelaar et al., 1977). Conditions were as follows: batch size 36 samples, Curie-point temperature 510°C, temperature rise time 0.1 s, total heating time 0.8 s, expansion chamber temperature 150°C, electron-impact ionisation at 15 eV, mass range 24—180, scan speed 10 scans s^{-1}, total number of averaged spectra

200. The mass to charge ratio (m/z) is expressed in atomic mass units. Samples were analysed in triplicate. A Curie-point high-frequency generator (model 9425; Fischer, 5309 Meckenheim bei Bonn, F.R.G.) was used to generate the magnetic field. The ferromagnetic wires were from Philips (5300 PB, Eindhoven, The Netherlands).

Multivariate treatment of the mass spectra by factor-discriminant analysis

The raw data, expressed in ion counts/mass channel, are normalised by expression of the mass intensities as percentages of the total ion counts. Multivariate analysis of the spectra was performed on files of selected spectra, using a modified ARTHUR package (Infometrix, Seattle, WA); the modifications and expansion of this package with linear discriminant analysis have been described by Hoogerbrugge et al. (1983). The principles of the application of this procedure to pyrolysis mass spectra have been described by Windig et al. (1983). The essential elements of the factor-discriminant analysis (f.d.a.) procedure are shown in Table III. After definition of the file (training set), an overall average spectrum (zero point) is calculated, which serves as the reference point for comparison of the individual spectra. This spectrum is also used for scaling of the data set. Positive and negative differences, with respect to this reference, are evaluated by the f.d.a. program. Covariant mass peaks are linearly combined to new independent variables (discriminant functions). The dissimilarity between the categories (groups of multiplicate spectra) is qualitatively expressed in these discriminant functions, which are represented graphically by reconstructed mass spectra. Dissimilarity is quantitatively expressed in discriminant function scores, which can be plotted as scores, curves or maps (in 2 dimensions).

TABLE III

Steps in the factor discriminant analysis for the Curie-point mass spectrometer based on an adapted ARTHUR program package expanded with discriminant analysis capabilities

(a) Choose the mass spectra for training set and test set.
(b) Determine overall average spectrum: zero point.
(c) Scale data on $(X-\overline{X})/\sigma$.
(d) Run principal components analysis: factors (groups of correlated mass peaks) are found and ordered according to the amount of variance explained.
(e) Quantify each factor in each mass spectrum: factor scores.
(f) Express each mass spectrum with factors as new variables. Average each category.
(g) Repeat c and d: discriminant functions (groups of correlated factors = groups of correlated mass peaks) are found, which describe differences between the categories.
(h) Quantify D-functions in each category and pyrolysis mass spectrum: D-scores.

RESULTS

Dynamics in loss of mass

The field experiments

A comparison of the initial nutrient content of *Nymphaea* leaves used in the field experiments reveals differences in nitrogen, phosphorus, potassium and sodium concentrations between the leaves harvested in the 2 systems and, to a lesser extent, between the 2 sampling days in the same system (Table IV). During the course of the decomposition experiments,

TABLE IV

Initial nitrogen, phosphorus, potassium and sodium levels (in μmol/g dry weight) of *Nymphaea alba* leaves used in the field experiments

	Oude Waal		Voorste Choorven	
	6 July	21 September	6 July	21 September
Nitrogen	1988	2080	1630	1683
Phosphorus	95.0	83.0	42.1	47.7
Potassium	341	377	213	222
Sodium	800	775	646	603

TABLE V

Range of chemical properties of the water from the Oude Waal and Voorste Choorven during the in situ litter bag experiments

Field experiment		Oude Waal		Voorste Choorven
		Summer	Autumn	Autumn
Alkalinity	meq l^{-1}	4.3—5.0	4.4—6.7	0.0—0.04
pH		7.2—8.2	7.5—8.7	3.9—4.4
Total N	μmol l^{-1}	45.6—59.6	52.8—150.0	95.6—500.0
NO_3^-/NO_2^-	μmol l^{-1}	0.7—1.8	0.2—10.0	0.9—21.0
NH_4^+	μmol l^{-1}	6.0—10.0	7.0—17.0	85.0—153.0
Total P	μmol l^{-1}	1.8—3.5	0.9—2.5	0.2—1.7
PO_4^{3-}	μmol l^{-1}	0.3—1.3	0.3—0.9	0.1—0.4
Na^+	μmol l^{-1}	1800—2360	1696—2190	242—360
K^+	μmol l^{-1}	90— 145	121— 130	36— 63
Mg^{2+}	μmol l^{-1}	281— 720	402— 683	26—108
Ca^{2+}	μmol l^{-1}	690—2420	1550—2360	40—400
SO_4^{2-}	μmol l^{-1}	300— 550	300— 420	210—330
Cl^-	μmol l^{-1}	1260—2760	1320—2412	210—362

TABLE VI

Temperature range of the overlying water from the Oude Waal and Voorste Choorven between the day of incubation (t_0) and the different sampling days (t_1—t_6) during the in situ litter bag experiments

	Oude Waal		Voorste Choorven
	Summer	Autumn	Autumn
t_0—t_1	18—22° C	16—22° C	16—19° C
t_1—t_2	19—23° C	13—16° C	12—15° C
t_2—t_3	18—22° C	12—13° C	11—14° C
t_3—t_4	17—20° C	6—13° C	9—13° C
t_4—t_5	14—19° C	5— 9° C	6—14° C
t_5—t_6	12—22° C		5—14° C

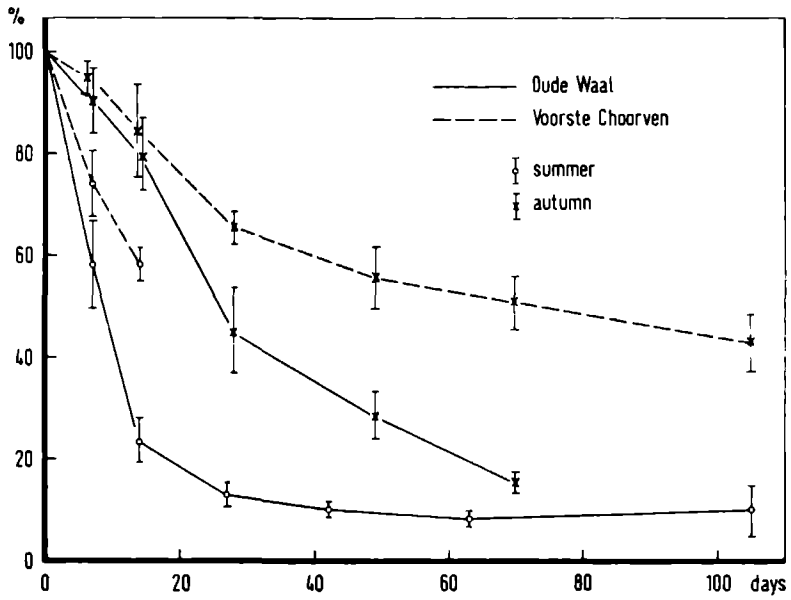

Fig. 2. The ash-free dry weight loss of decomposing *Nymphaea alba* leaves as influenced by the season and the trophic status of the system. The Voorste Choorven is an acid moorland pool and the Oude Waal an alkaline eutrophic oxbow lake. The dots and bars represent mean values of residual weight and standard deviations.

there were also considerable differences in the physico-chemical conditions of the Oude Waal and Voorste Choorven water (Tables V and VI). During the whole sampling period, the water from the Oude Waal was alkaline and fairly rich in phosphorus, potassium, sodium and calcium. In autumn, the Oude Waal water had lower temperatures and higher nitrogen levels than in summer. In the Voorste Choorven water, low pH and very low alkalinity values were measured compared with the Oude Waal. Furthermore, high nitrogen (particulary ammonium) and relatively low phosphorus and potassium concentrations were measured here.

TABLE VII

The decay parameter (k), its standard error (s.e.) and coefficient of determination (C.D.) of the exponential model when fitted to the decomposition data of the field experiments

	$W(t) = W(o) \exp - k.t.$			
	k	s.e.	C.D.	n
Oude Waal, summer	0.0841	0.0057	0.9339	35
Oude Waal, autumn	0.0247	0.0012	0.9512	30
Voorste Choorven, summer	0.0401	0.0023	0.9274	15
Voorste Choorven, autumn	0.0101	0.0005	0.8715	35
Concrete tank, Oude Waal material	0.0828	0.0057	0.9274	24
Concrete tank, Voorste Choorven material	0.0529	0.0036	0.9006	24

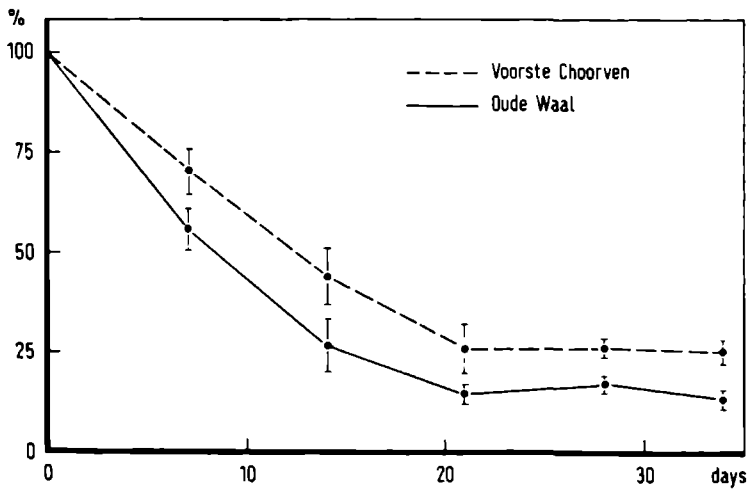

Fig. 3. The ash-free dry weight loss of decomposing *Nymphaea alba* leaves which originated from an acid moorland pool (Voorste Choorven) and an alkaline eutrophic oxbow lake (Oude Waal) and which were transplanted to the water of a concrete tank.

A comparison of the relative amounts of residual organic mass of decomposing leaves of *Nymphaea alba* reveals differences in breakdown patterns between the experiments in the 2 systems and seasons studied (Fig. 2). In both seasons, the breakdown of the decomposing *Nymphaea* leaves (as measured with the exponential model) was significantly faster in the Oude Waal than in the Voorste Choorven ($P < 0.01$) (Table VII). When the results of the 2 seasons are compared, it is found that the weight loss parameter (k) is significantly higher ($P < 0.01$) for the summer experiments, indicating faster breakdown at higher temperatures.

The *Nymphaea* leaves originating from 2 different localities had different breakdown patterns in water from the same outdoor concrete tank (Fig. 3); the *Nymphaea* leaves from the Oude Waal had a significantly higher weight loss rate ($P < 0.01$) than those from the Voorste Choorven (Table VII). In the concrete tank, the different breakdown rates can only be attributed to differences in chemical composition between the leaves harvested in the Oude Waal and Voorste Choorven.

The laboratory experiments

The *Nymphaea* leaves which were harvested at different localities or different periods of the year had different weight loss rates and/or decay patterns under the same environmental conditions in the laboratory (compare control treatments in Table VIII). The leaves which were used for the different experiments also differed in their initial nutrient content (Table IX). Low nitrogen, phosphorus and potassium concentrations were found, particularly in the leaves harvested in late autumn (Experiment IV), which can most probably be attributed to resorption and translocation of these nutrients to the root stocks prior to mass senescence of the leaves. The high sodium levels in the leaves harvested for Experiment IV indicate that they were not in a decomposing state. During breakdown, sodium usually leaks out very fast from decomposing macrophyte material (see e.g., Brock, 1984). A clear correlation between the initial concentration of a certain element in the leaves (e.g., nitrogen) and the weight loss rate of that plant material could not be found (Table IX). The differences in the decay patterns of the *Nymphaea* leaf discs in the control treatments must be due to differences in the total chemical composition of the plant material.

The presence of bicarbonate in the medium stimulated the weight loss of *Nymphaea* leaf discs (at least in the initial phase) when compared with the corresponding control treatment (Tables VIII and Fig. 4). The weight loss rates of the leaf material were significantly higher ($P < 0.01$) in the treatments with 5000 μmol HCO_3^- l^{-1} than in the media with lower bicarbonate concentrations. From Experiment III (Table VIII), it appears that the weight loss rate of the *Nymphaea* leaf discs in the 5000 μmol HCO_3^- treatment (with a pH value of approximately 8) was significantly higher ($P < 0.01$) than that of the pH 8 (NaOH) treatment. This phenomenon can most probably be attributed to the much higher buffer capacity of the bicarbonate solution used compared with that of the pH 8 (NaOH) medium.

TABLE VIII

The relative amounts of residual weight of decomposing *Nymphaea alba* in the various treatments of the laboratory experiments as well as the decay parameter (k), its standard error (s.e.) and coefficient of determination (C.D.) of the fitted exponential model

	% residual weight ± standard deviation				$W(t) = W(o) \exp - k.t.$			
	7 days	14 days	21 days	28 days	k	s.e.	C.D.	n
Experiment I								
Control	67.6 ± 3.4	34.0 ± 5.0	18.7 ± 1.6	14.8 ± 1.1	0.0711	0.0026	0.8992	20
HCO_3^- 500 µmol l^{-1}	60.6 ± 3.8*	35.9 ± 4.4	15.9 ± 0.8*	14.9 ± 1.5	0.0751	0.0022	0.9875	20
HCO_3^- 1000 µmol l^{-1}	49.0 ± 3.4*	24.5 ± 6.0*	11.2 ± 1.8*	14.5 ± 0.6	0.0972*	0.0040	0.9795	20
HCO_3^- 5000 µmol l^{-1}	43.8 ± 4.5*	17.7 ± 2.0*	13.9 ± 0.8*	11.7 ± 1.5*	0.1107*	0.0048	0.9803	20
NO_3^- 10 µmol l^{-1}	68.8 ± 5.1	30.3 ± 2.8	15.5 ± 3.2	11.9 ± 1.9*	0.0759	0.0037	0.9688	20
NO_3^- 100 µmol l^{-1}	62.1 ± 4.7	28.9 ± 10.3	10.4 ± 1.2*	12.0 ± 2.5°	0.0842*	0.0045	0.9661	20
NH_4^+ 10 µmol l^{-1}	63.0 ± 5.9	35.5 ± 2.2	12.2 ± 1.9*	14.1 ± 1.2	0.0766	0.0031	0.9774	20
NH_4^+ 100 µmol l^{-1}	56.7 ± 3.5*	26.5 ± 4.4°	15.3 ± 2.9°	15.1 ± 1.1	0.0852*	0.0030	0.9834	20
PO_4^{3-} 0.5 µmol l^{-1}	66.2 ± 5.2	33.3 ± 7.0	19.2 ± 2.5	14.1 ± 1.6	0.0723	0.0028	0.9775	20
PO_4^{3-} 5.0 µmol l^{-1}	66.7 ± 3.8	36.8 ± 3.1	20.4 ± 4.4	17.9 ± 1.4*	0.0675	0.0022	0.9833	20
Experiment II								
Control	76.8 ± 3.3	45.7 ± 6.7	36.5 ± 5.4	41.2 ± 2.6	0.0428	0.0027	0.8992	20
HCO_3^- 500 µmol l^{-1}	73.0 ± 3.7	46.6 ± 2.6	32.7 ± 4.0	19.4 ± 0.7*	0.0536*	0.0015	0.9854	20
HCO_3^- 1000 µmol l^{-1}	68.2 ± 4.5*	44.2 ± 3.4	28.7 ± 4.8°	25.0 ± 1.9*	0.0557*	0.0017	0.9809	20
HCO_3^- 5000 µmol l^{-1}	63.6 ± 3.8*	32.1 ± 5.8*	19.6 ± 3.1*	13.3 ± 1.0*	0.0746*	0.0024	0.9844	20
NO_3^- 10 µmol l^{-1}	72.9 ± 3.0	51.4 ± 5.2	32.2 ± 3.2	21.7 ± 2.9*	0.0510*	0.0015	0.9822	20
NO_3^- 100 µmol l^{-1}	75.6 ± 1.0	43.4 ± 6.7	21.9 ± 2.9*	11.1 ± 0.8*	0.0625*	0.0034	0.9573	20
PO_4^{3-} 0.5 µmol l^{-1}	74.8 ± 1.7	51.0 ± 5.3	41.8 ± 5.1	36.2 ± 1.9*	0.0413	0.0022	0.9227	20
PO_4^{3-} 5.0 µmol l^{-1}	73.4 ± 2.8	51.2 ± 8.0	33.3 ± 7.1	31.2 ± 5.9*	0.0468	0.0021	0.9539	20
Experiment III								
Control	65.9 ± 7.0	44.4 ± 6.3	30.8 ± 6.1	17.6 ± 2.4	0.0586	0.0022	0.9720	20
pH 3 (HCl)	71.1 ± 1.5	53.7 ± 5.4°	46.8 ± 5.2*	44.5 ± 1.6*	0.0365*	0.0019	0.9031	20
pH 8 (NaOH)	62.5 ± 4.7	48.8 ± 6.1	35.6 ± 4.6	21.6 ± 3.1	0.0537°	0.0021	0.9640	20
HCO_3^- 5000 µmol l^{-1} (pH ≅ 8)	55.9 ± 6.1°	29.7 ± 4.4*	20.0 ± 3.3*	18.9 ± 1.8	0.0781*	0.0036	0.9659	20
NO_3^- 100 µmol l^{-1}	66.1 ± 4.6	35.5 ± 4.7°	28.8 ± 3.0	19.4 ± 4.5	0.0633	0.0024	0.9741	20
HCO_3^- 5000 µmol l^{-1} + NO_3^- 100 µmol l^{-1}	57.4 ± 0.9°	25.9 ± 3.1*	14.9 ± 2.2*	15.6 ± 0.9	0.0851*	0.0031	0.9819	20
PO_4^{3-} 5 µmol l^{-1}	65.5 ± 1.8	41.7 ± 6.1	28.7 ± 4.4	19.0 ± 3.6	0.0605	0.0018	0.9836	20
NO_3^- 100 µmol l^{-1} + PO_4^{3-} 5 µmol l^{-1}	65.2 ± 4.5	34.0 ± 1.5*	23.4 ± 3.2°	18.4 ± 2.7	0.0680*	0.0022	0.9817	20
Experiment IV								
Control	58.8 ± 2.5	47.1 ± 1.5	40.2 ± 2.7	35.8 ± 2.7	0.0478	0.0018	0.9373	20
pH 3 (HCl)	61.9 ± 2.4	52.6 ± 1.6*	49.0 ± 2.0*	46.1 ± 2.4*	0.0372*	0.0028	0.7878	20
pH 8 (NaOH)	63.0 ± 2.6	48.9 ± 1.3	42.9 ± 3.4	35.9 ± 3.0	0.0445	0.0023	0.9187	20

*Significantly different from the control treatment ($P < 0.01$); ° significantly different from the control treatment ($P < 0.05$).

TABLE IX

Initial nitrogen, phosphorus, potassium and sodium levels (in μmol/g dry weight) of *Nymphaea alba* leaves used in the various laboratory decomposition experiments as well as the decay rates (k) of the control treatments. The leaves for Experiment I were harvested in the Oude Waal and for the other experiments in the Voorste Choorven

		Initial nutrient level				Decay rate
		N	P	K	Na	(k)
Experiment I	(21 July)	1868	93	321	800	0.0711
Experiment II	(10 September)	1621	40	218	731	0.0428
Experiment III	(15 October)	2054	42	221	789	0.0586
Experiment IV	(9 November)	1169	15	165	930	0.0478

The weight loss rates of the *Nymphaea* leaf discs were significantly smaller ($P < 0.01$) in the pH 3 (HCl) treatments than in the control (with a pH value of approximately 6) and pH 8 (NaOH) treatments (Table VIII), indicating a slower weight loss in acidified water (see also Fig. 4). In Experiment III, the breakdown rate of the *Nymphaea* material in the pH 8 (NaOH) treatment was smaller ($P < 0.05$) than in the case of the control treatment (with a pH value of approximately 6), while in Experiment IV, the breakdown rates of the *Nymphaea* leaf discs in the pH 8 (NaOH) treatment and the control medium did not differ significantly.

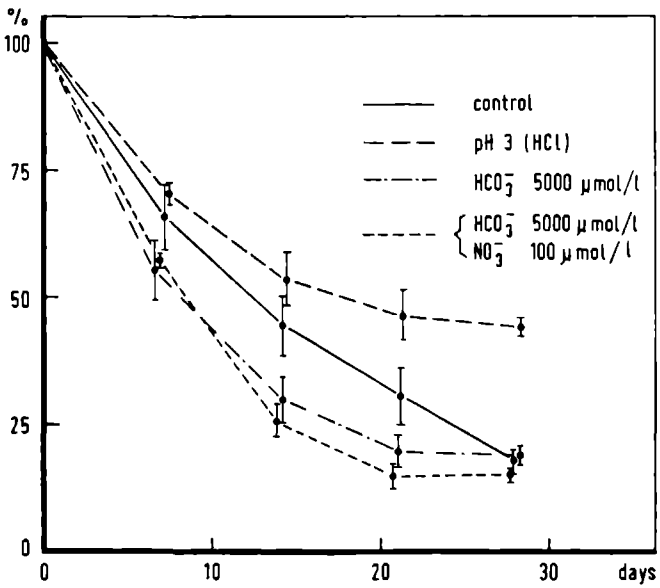

Fig. 4. The dry weight loss of decomposing leaf discs of *Nymphaea alba* in several media in the laboratory.

Addition of nitrogen to the medium resulted in some cases in a moderate increase in the breakdown of *Nymphaea* material (Table VIII). In Experiment I, the weight loss rates of the leaf discs in the treatments with a corresponding concentration of nitrogen (nitrate or ammonium) did not differ significantly. In Experiment I, in which plant material with a relatively high initial nitrogen content was used, a significantly higher breakdown rate was obtained in the 100 μmol nitrate or ammonium treatments, but not in the treatments with 10 μmol NO_3^- or NH_4^+. In Experiment II, in which plant material with the lowest initial nitrogen content was used, both the 10 μmol and 100 μmol NO_3^- treatments resulted in a significantly higher breakdown rate of the leaf discs compared with the control treatment. In Experiment III, in which the *Nymphaea* material had the highest initial nitrogen concentration, the breakdown rates of the leaf discs in the control and 100 μmol NO_3^- treatments did not differ significantly. These results suggest that the possible decay-stimulating effect of nitrogen in the medium is influenced by the initial nitrogen content of the plant material under investigation.

Addition of phosphorus to the basic medium did not result in a faster breakdown of the *Nymphaea* leaf discs (Table VIII). Although in Experiment III, enrichment of the medium with nitrate or orthophosphate alone did not result in a significantly higher breakdown rate, the weight loss rate of the leaf discs was significantly higher ($P < 0.01$) in a medium enriched with both orthophosphate and nitrate compared with the control treatment. This experiment illustrates that the effect of a certain chemical parameter on the breakdown of macrophyte material may be dependent on interaction with other chemical parameters.

In Experiment III, the highest weight loss rate of the decomposing leaf discs was found in a medium enriched with bicarbonate and nitrate (Fig. 4 and Table VIII). However, this weight loss rate did not differ significantly from that of the 5000 μmol HCO_3^- treatment. Nevertheless, after 21 and 28 days of incubation the relative amounts of residual weight in the medium enriched with both bicarbonate and nitrate were significantly lower ($P < 0.01$) than those of the 5000 μmol HCO_3^- treatment. Although bicarbonate was the dominant factor, the influence of nitrate was large enough for minor modifications of the breakdwon pattern of the *Nymphaea* material in the medium enriched with HCO_3^- and NO_3^-.

Organic matter changes during decomposition

Overall changes in organic matter composition of particulate residues of decomposing *Nymphaea alba* leaves are expressed as discriminant function scores in Fig. 5A and B. These figures delineate the relative change in organic matter composition of the particulate residues during the course of the field and laboratory experiments. The discriminant function scores were calculated from the first (most important) discriminant function, which

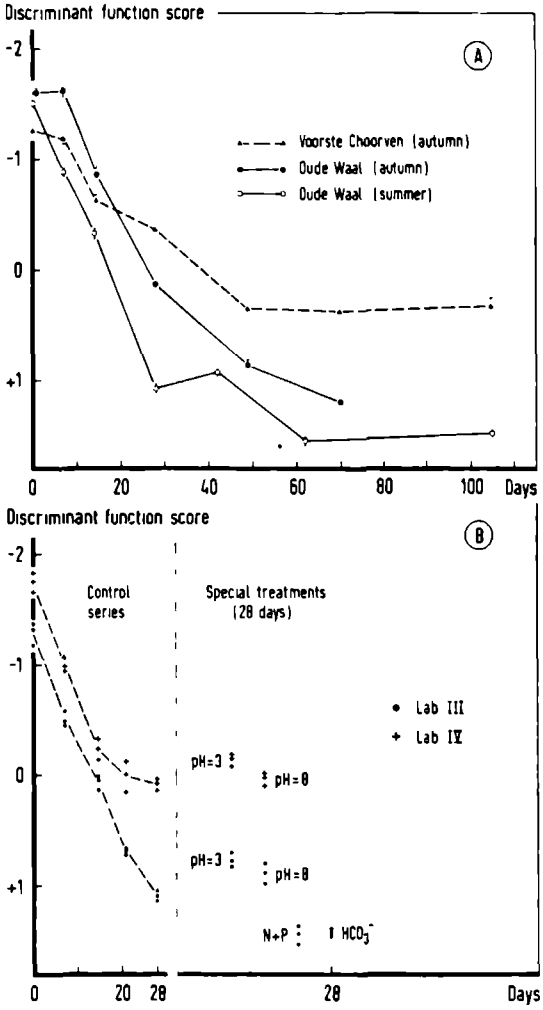

Fig. 5. Overall changes in organic matter composition of the particulate residues of decomposing *Nymphaea alba* leaves under field (A) and laboratory (B) conditions, expressed as discriminant function scores calculated from a file of pyrolysis mass spectra.

accounted for about 50% of the characteristic variance in the data set. The range in these scores for each sample is given by bars which describe compositional and instrumental variability. A high inclination of the score curve indicates a rapid change in organic matter composition of the particulate residues, whereas a horizontal course points to a constant composition.

There are clear differences in organic matter composition of the particulate residues between the experiments in the 2 systems and seasons as decay progresses (Fig. 5A). A surprisingly good correlation is evident when

the curves in Fig. 5A are compared with the weight loss curves shown in Fig. 2. The organic matter composition of the particulate residues in the Oude Waal summer experiment changes most rapidly and is accompanied by the highest rate of weight loss. The material from the Oude Waal autumn experiment does not show a change in organic matter composition during the first week. This clear lag phase is probably caused by the lower temperatures of the water. In autumn, the change in organic matter composition is slower than in summer. The organic matter composition of the coarse detritus after 70 days in the Oude Waal autumn experiment is similar to a sample after decay of about one month in the Oude Waal summer experiment (see also later in Fig. 7). The material from the Voorste Choorven (only autumn samples available) shows very different behaviour compared with that from the Oude Waal. In the Voorste Choorven, the change in organic matter composition is slower and stops during the second month of incubation. This corresponds to the low weight loss rate (k) and the high amount of residual organic matter at the end of the experiment (Fig. 2). The discriminant function scores demonstrate that differences in organic matter composition of the leaves from the Oude Waal and Voorste Choorven were relatively small at the start of incubation compared to the changes induced by the decomposition process. This suggests that the differences in decomposition between the Oude Waal and Voorste Choorven are mainly caused by environmental factors.

Differences in environmental conditions were minimised in the control treatments of the laboratory decomposition experiments. Standardized water conditions were employed where a constant temperature of 20°C mimics a summer decomposition regime. The curve of the change in organic matter composition of the coarse detritus in the control treatment of Laboratory Experiment III (Fig. 5B) closely follows the curve of the Oude Waal summer experiment (Fig. 5A). The curve for the control treatment of Laboratory Experiment IV (Fig. 5B) levels off after 2 weeks and the spectra of organic matter composition of the residues after 21 and 28 days are similar. A good correlation of these data with weight loss results is evident from Table VIII.

Experiments in which the trophic conditions and/or the pH of the water were changed with respect to the controls, were performed to evaluate the influence of the environment on decomposition of *Nymphaea* leaves. Of these special treatments, the scores of the organic matter composition of the particulate residues after 28 days of incubation are plotted in Fig. 5B. In Laboratory Experiment III, acidification of the medium results in stagnation of the change in organic matter composition; the spectrum of the particulate residue after 4 weeks of decomposition at pH 3 is similar to the spectrum of the residue after 3 weeks in the control medium. A pH 8 medium also leads to a somewhat smaller change in organic matter composition of the coarse detritus compared to that of the control medium (pH 6). The relative position of the material which decayed in water en-

riched with bicarbonate or nitrate-orthophosphate points to an acceleration in the change of organic matter composition due to the addition of these nutrients. In accordance, a faster weight loss is observed under the more eutrophic and alkaline conditions (see Table VIII).

The effect of different pH on the decomposition of the plant material used for Laboratory Experiment IV was smaller than in Laboratory Experiment III; nevertheless, acidification again resulted in a stagnation in the change of organic matter composition (Fig. 5B).

Changes in organic matter composition in the particulate residues of *Nymphaea* leaves develop during the decomposition process. The degree of compositional change is determined by the season and site-dependent factors. These factors influence both the composition of the original plant material and the decomposer community. The nature of the organic matter composition of the original plant material used in the various experiments can be evaluated by factor-discriminant analysis of the starting material. A tentative chemical interpretation of the discriminant function spectra of subfiles of the field and laboratory experiments should indicate the nature of the chemical changes in composition during the decay process.

Chemical differences between the particulate residues of Nymphaea alba

General remarks

Definite chemical conclusions cannot be easily drawn from pyrolysis mass spectra because the mass spectral information is accumulated in one finger print. Precise structural identification of each pyrolysis product requires chromatographic separation of the pyrolysate followed by mass spectral characterisation of the pure compounds, a technique known as pyrolysis gas chromatography mass spectrometry (pygcms). However, a number of plant polymers are known to generate pyrolysis products which can be recognised by molecular ions and fragment ions in pyrolysis mass spectra (Meuzelaar et al., 1982). Such peak series have been compared with pure standards and with results from pygcms-analysis (Van der Kaaden et al., 1983; Saiz-Jimenez and De Leeuw, 1985). Thus pyrolysis mass spectra and spectra resulting from factor discriminant analysis can be evaluated chemically, although assignments remain tentative.

The fresh plant material

Pyrolysis mass spectra of fresh plant material from the field and laboratory experiments discussed above were compared using factor-discriminant analysis. The result is shown in Fig. 6. The general organic matter composition of *Nymphaea* plant material is represented by the zero point spectrum in Fig. 6A, which shows the mass peaks indicative for carbohydrates such as simple sugars, amylose, cellulose and hemicellulose (the m/z series 31, 32, 43, 55, 58, 60, 72, 74, 82, 84, 95, 96, 97, 98, 102, 110, 112, 114, 126, 128, 144), lignins (the m/z series 94, 108, 110, 120, 122, 124, 138,

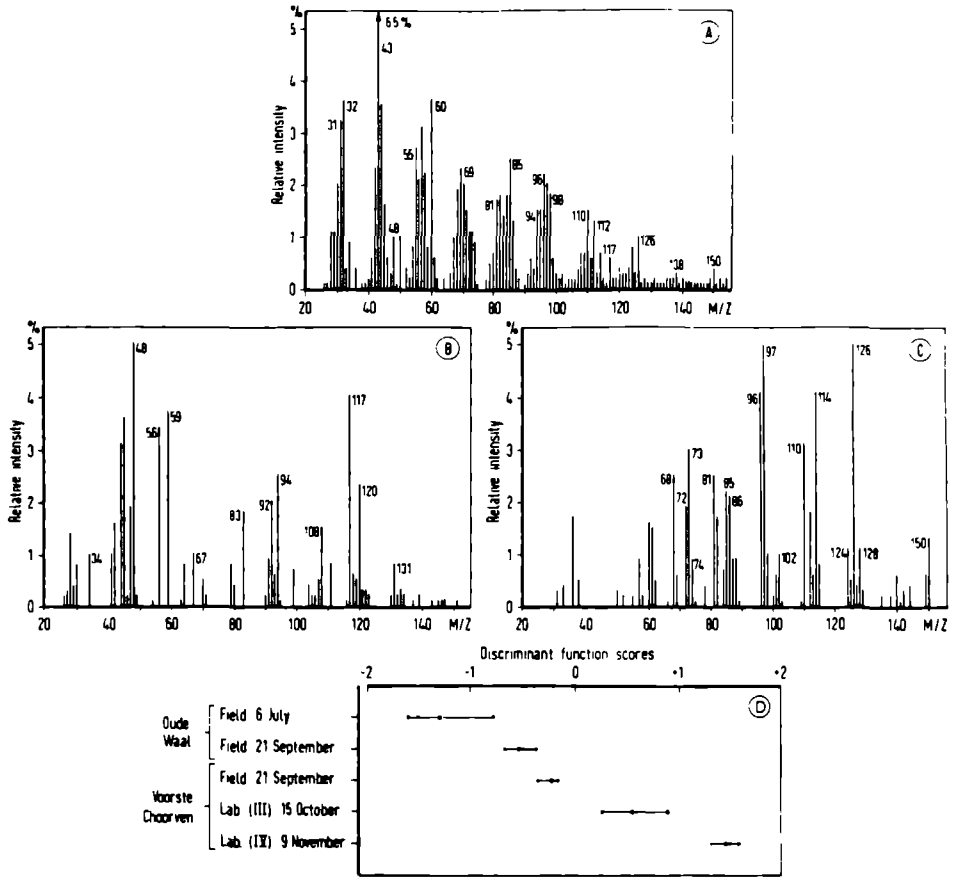

Fig. 6. Pyrolysis mass spectra of fresh leaves of *Nymphaea alba* used in the field and Laboratory Experiments (III and IV): (A) overall average spectrum; (B) reconstructed mass spectra of the negative part of the first discriminant function (indicative for proteinaceous material); (C) reconstructed mass spectra of the positive part of the first discriminant function (indicative for the lignocellulose complex); (D) discriminant function scores which express the quantitative differences in organic matter composition between the leaves, harvested at different times in the Oude Waal or Voorste Choorven.

150, 152, 154, 164, 166), and proteinaceous materials (the m/z series 34, 48, 56, 59, 67, 81, 83, 92, 94, 97, 108, 117, 131) as discussed before for several aquatic macrophytes (Boon and Haverkamp, 1982; Boon et al., 1982; 1983b). The mass peaks in the discriminant function spectra (Fig. 6B, C) describe the qualitative differences between the spectra of the various samples with respect to the zero point spectrum (Fig. 6A). The differences between the spectra of the fresh plant material used in the various experiments are described quantitatively in the scores in Fig. 6D. A relative enrichment in proteinaceous material is deduced from the mass peaks in

function D_1^- (Fig 6B) and expressed for each sample as negative score values in Fig 6D, whereas positive scores point to an enrichment in pentose and hexose carbohydrates (probably from hemicellulose and cellulose) and in lignin as deduced from the spectrum D_1^+ in Fig. 6C.

Thus, plant material used in the Oude Waal summer experiment, with a strongly negative score in Fig. 6D, was relatively protein rich The leaf material used in Laboratory Experiment IV, with high positive score values, has the lowest signals for protein material and the highest signals for structural carbohydrates and lignins in its pyrolysis mass spectrum. The samples from the Oude Waal and Voorste Choorven collected on 21 September are quite similar in organic matter composition, even after consideration of the second and third discriminant function.

There is a remarkable correlation of the scores in Fig. 6D and the time of collection of the samples. In both systems, a general trend towards less proteinaceous material and more structural carbohydrates and lignin later in the season is evident. It is a generally known strategy in plants to resorb certain useful resources to the root system late in the season (e.g., Thimann, 1978); our data appear to demonstrate this process.

Clearly the differences in initial organic matter composition must have a bearing on the rate of weight loss and compositional change. Fig. 5B demonstrates that under identical laboratory conditions the leaves collected and incubated in November (Experiment IV) decomposed with much more difficulty than the October leaves (Experiment III). This must relate to the higher initial structural carbohydrate and lignin levels in the November plant material. On the other hand, the Oude Waal and Voorste Choorven plant samples collected in September have a similar initial organic matter composition. Therefore, the observed differences in weight loss and chemical change of decaying *Nymphaea alba* leaves between the Oude Waal and Voorste Choorven are mainly caused by differences in the ambient environment between these sites.

Field samples

The pyrolysis mass spectra of samples from the 3 field experiments were compared by factor-discriminant analysis in order to understand the differences in decomposition patterns of the *Nymphaea* leaves in the 2 systems and seasons studied. Figure 7 shows a score plot of 2 discriminant functions which together describe 76% of the characteristic variance. It appears that the summer and autumn samples from the Oude Waal follow a similar path of compositional change, whereas the Voorste Choorven material has its own route. The organic matter composition of the latter seems to remain constant after about one month. This is not the case with the material from the Oude Waal, although a difference between summer and autumn is evident in the rate of change of the organic matter composition of the coarse detritus. This phenomenon is presumably caused by temperature differences in the water during the experiments.

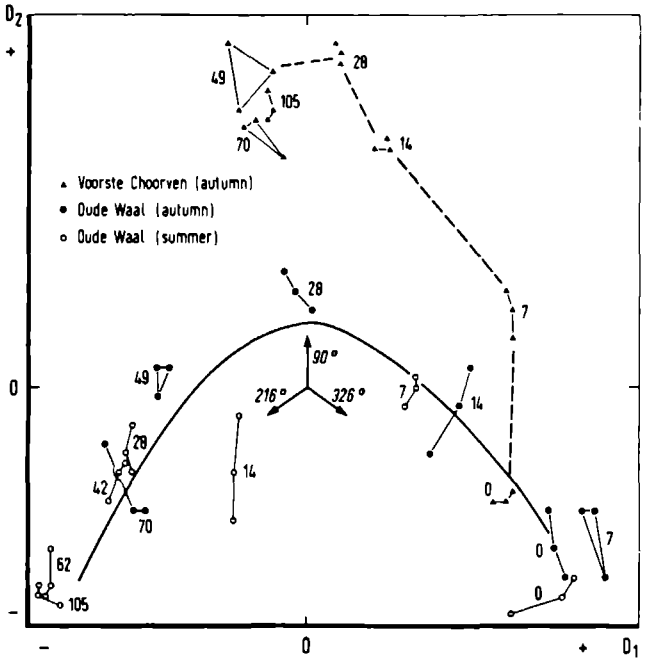

Fig. 7. Discriminant function score plot of pyrolysis mass spectra of particulate residues from decomposing *Nymphaea* leaves in the Oude Waal (summer and autumn) and Voorste Choorven (autumn). Samples are coded by their period of incubation (in days). Vectors at 90, 216 and 326° through the zero point are the directions used for graphical rotation of the discriminant functions shown in Fig. 8.

The difference between the routes of compositional change is best expressed by the discriminant function projected on the vectors drawn through the respective clusters of the final stages of decomposing Voorste Choorven (vector at 90°) and Oude Waal material (vector at 216°) and through the initial stages of decomposition (vector at 326°). Figure 8 shows the reconstructed mass spectra of the discriminant functions along these directions which were obtained by graphical rotation of the discriminant functions (see Windig et al., 1981) over the angle determined from the discriminant score map in Fig. 7. Figure 8A shows the mass peaks which decrease in relative intensity in the pyrolysis mass spectra of the starting material in the initial stages of decomposition. The chemical information in this spectrum does not point to one particular substance, but rather to various types of organic matter including proteinaceous material (m/z 67, 81, 92, 94, 108, 117, 131), intracellular carbohydrates such as oligosaccharides and starches (m/z 74, 82, 84, 98, 112, 126) and some phenolic substances (m/z 94, 110, 120, 124, 150). The mass peaks 50 and 52 are from methylchloride, which is very often formed by pyrolysis of fresh plant material. This compound is a reaction product of chloride salts and methyl groups

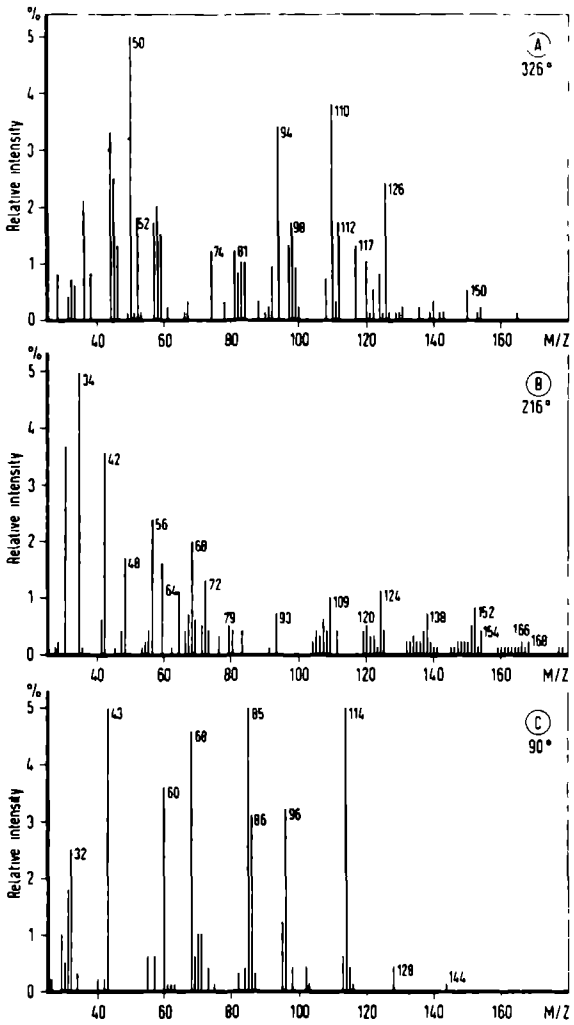

Fig. 8. Reconstructed mass spectra which describe the discriminating mass peaks in pyrolysis mass spectra of *Nymphaea* leaves in the initial stage of decomposition (A) and the final stages of decomposition in the Oude Waal (B) and Voorste Choorven (C). These spectra were obtained by graphical rotation of the first discriminant function in the D_1D_2-plane over 326° (A), 216° (B) and 90° (C).

released from an unknown substrate during pyrolysis. The chlorides may be a good indicator of the inorganic salts in the plant material. They are rapidly lost during the initial phases of decomposition.

Figure 8B represents the reconstructed mass spectrum of the discriminant function which describes the mass peaks of increased relative intensity in the particulate residues at the end of the incubation period in the Oude Waal. Mass peaks m/z 34 (H_2S), 48 (CH_3SH), 64 (S_2 or SO_2) and 76 (CS_2)

point to an accumulation of reduced sulphur compounds in the residues, probably a sign of anaerobic conditions in the decomposing plant material. The series m/z 124, 138, 152, 154, 166 and 168 is characteristic of methoxyphenols which indicate an accumulation of lignins of the coniferyl and syringyl type in the particulate matter.

Figure 8C shows the discriminating characteristics in the mass spectra of the Voorste Choorven particulate residues after about one month up to 105 days of incubation. The spectrum represents a carbohydrate rich in pentose units, probably some sort of xylan or araban in the hemicellulose fraction, which accumulates in the residues. The accumulation of this polymer in the particulate residues in the Voorste Choorven, indicates a missing link in the decomposer community and leads to a marked inhibition of weight loss. The accumulated polymer appears to preclude any further change in the composition of the residues after about one month of incubation. This phenomenon did not occur in the Oude Waal experiments, which indicates that the water chemistry is most important since no major differences in the starting material from the 2 systems could be demonstrated.

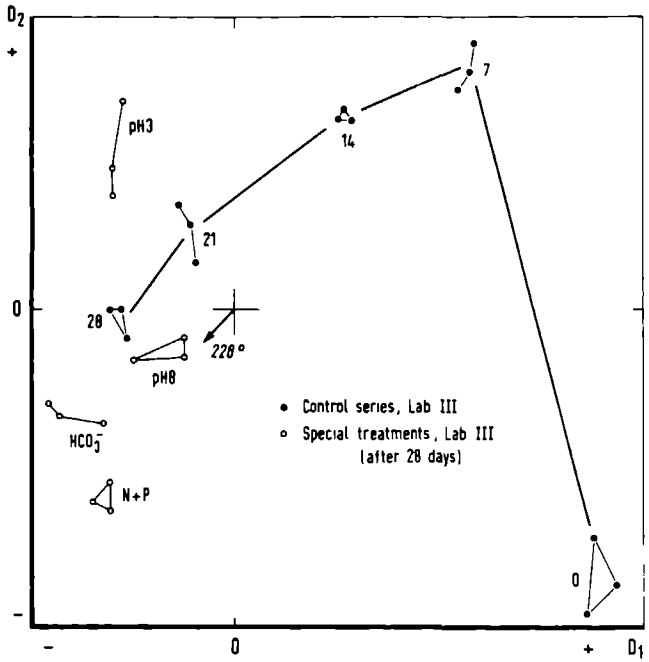

Fig. 9. Discriminant function plot of pyrolysis mass spectra of particulate residues from *Nymphaea* leaves decomposing under laboratory conditions (Experiment III). The position of the residues from the complete control series (coded in days) and the residues after 28 days of decomposition in pH 3 and pH 8 media and in media enriched with bicarbonate (HCO_3^-) and nitrate-orthophosphate (N+P) is plotted.

Laboratory experiments

Figure 9 shows a 2-dimensional (2D) plot of the particulate residues of the Laboratory III experiment. Most of the sample points lie slightly above the D_1D_2 plane, except for the material incubated at time zero and the residue after 4 weeks under pH 3 conditions. The latter sample cluster is far below the D_1D_2 plane at an angle of 64° with respect to the zero point.

The position of the freshly-incubated material with respect to the residues after one and 2 weeks, demonstrates that a significant change in organic

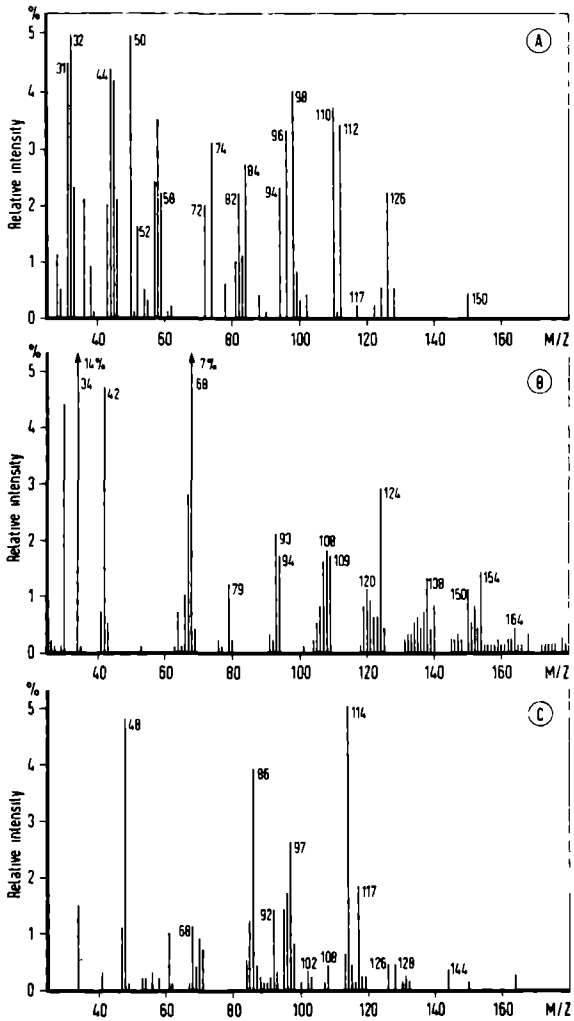

Fig. 10. Reconstructed mass spectra describing the discriminating mass peaks in pyrolysis mass spectra of decomposing *Nymphaea* leaves in Laboratory Experiment III: (A) the initial stages of decomposition; (B) the final stages of decomposition in bicarbonate and nitrate—orthophosphate enriched water; (C) the final stages of decomposition in a pH 3 medium.

matter composition takes place early in the experiment. The discriminant function spectrum in Fig. 10A describes these early changes and points to a loss of non-structural carbohydrates, proteinaceous material and phenolic compounds. A comparison of Figs. 8A and 10A demonstrates that similar processes occur in the initial stages of decomposition under field and laboratory conditions. Although at different magnitudes, most of the mass spectral characteristics are seen in both figures.

Graphical rotation of the discriminant function in the D_1D_2 plane over 228° leads to the spectrum shown in Fig. 10B. This spectrum is a projection on a vector through the cluster of the residues from bicarbonate-rich and from nitrate-orthophosphate-enriched water. The spectrum is dominated by m/z 68 of unknown meaning. Many mass peaks in this spectrum, e.g., m/z 94, 108, 120, 124, 138, 150, 152, 154, 164, 168, point to lignin material which has accumulated in the residues. The same mass peaks were found to increase in spectra of the residues from the Oude Waal summer and autumn experiments (compare with Fig. 8B). Remarkably, the mass peaks m/z 30, 34 and 42 are found to be covariant with the lignin mass peaks in Fig. 8B as well as Fig. 10B. However, mass peak m/z 68 is much less intense in Fig. 8B which demonstrates that some differences must exist between field and laboratory conditions.

The spectrum in Fig. 10C is a result of graphical rotation in 3 dimensions and describes the discriminating characteristics of the particulate residues after 4 weeks under pH 3 conditions. Mass peak m/z 114 points to a carbohydrate with pentose units (probably from hemicellulose) which accumulates under these conditions. Also a number of characteristic masses for protein material (from microorganisms?), e.g., m/z 48, 92, 117/131, are present in this spectrum. A number of the mass peaks which characterise the Voorste Choorven field samples after about one month (compare Fig. 8C) are also seen in Fig. 10C. This is again an indication that acid conditions lead to a deviation in the routes of plant material decomposition.

The results of Laboratory Experiment IV will be mentioned only briefly. The initial changes in composition greatly resembled the results obtained in Laboratory Experiment III. After 21 days and later, an accumulation of a pentose-rich carbohydrate becomes obvious. The mass spectral characteristics are similar to those found for the Voorste Choorven field samples. The experiment at pH 3 resulted in a particulate residue after 4 weeks which differed from the residues of all other treatments in Experiment IV. The differences were quite similar to those found for the Laboratory III Experiment.

DISCUSSION

Methodology

In the present study, litter bags were employed to investigate the breakdown of *Nymphaea alba* leaves in the field and in the laboratory. An im-

portant drawback of the application of litter bags in the ambient water of natural systems and in the water of open flow-through aquaria in the laboratory, is that the fate of the fine particulate and dissolved organic detritus is not studied. An alternative might be to study the breakdown of the leaves in closed systems (e.g., bottles or containers). However, an important disadvantage of the use of bottles in decomposition studies is that the physico-chemical properties (e.g., oxygen level, pH value, nutrient concentration) of the water in the bottles are dramatically altered during the course of the decomposition experiments, particularly when the volume of the water in the containers is relatively small and the amount of detritus relatively large. Furthermore, in such bottles an accumulation of metabolic products which inhibit the activities of decomposers may occur. It was our objective to study the effect of the water chemistry on the decay of macrophyte material. Therefore, the chemical composition of the water in each treatment was kept constant in the open flow-through aquaria throughout the whole decomposition experiment. Litter bags were used because in the mesh bags the detritus is not isolated from the surrounding water. Our decomposition experiments give a good insight only in the breakdown of the coarse macrophyte detritus in the overlying water of aquatic ecosystems, as a result of these methodological choices.

The general decay pattern of Nymphaea alba *leaves*

The decomposing leaf blades of *Nymphaea alba* showed a relatively fast fragmentation in all our experiments. In general, fragmentation was faster when the weight loss rate was higher. Parts of the major veins, fragments of the epidermis and trichosclereids remained recognizable in the particulate residues.

During the first 10—30 days of incubation, a pronounced weight loss and a rapid change in organic matter composition of decaying *Nymphaea* leaves was observed in all field and laboratory experiments. Certain carbohydrates (probably non-structural ones such as oligosaccharides and starches), proteinaceous material and phenolic compounds, particularly, leached out and/or were metabolized at high rates by microorganisms during the initial decay period. In a later stage (after approximately 10—30 days), the changes in weight and organic matter composition of the particulate residues were relatively small. Then an accumulation of structural carbohydrates and lignin could be observed. Structural carbohydrates (cellulose and hemicellulose) and lignin largely originate from the cell wall fraction of *Nymphaea* leaves. The rate of disappearance of these structural carbohydrates from the particulate residues was dependent on the physico-chemical properties of the ambient water.

Interspecific variability exists between decay rates of aquatic vascular plants, which can be explained by differences in chemical composition between different species. In the oxbow lake environment in the vicinity

of Nijmegen (The Netherlands), the decomposition of 3 species of floating-leaved macrophytes was studied; in summer the rate of weight loss of the floating leaves of *Nymphaea alba* (k = 0.084) was smaller than that of the leaves of *Nymphoides peltata* (Gmel.) O. Kuntze (k = 0.091) and higher than that of *Nuphar lutea* (L.) Sm. (k = 0.066) (this study; Brock, 1984; Brock et al., 1985). In general, floating-leaved macrophytes show a faster weight loss and a faster change in organic matter composition during their decay than most submerged and, in particular, emergent macrophytes (see e.g., Godshalk and Wetzel, 1978; Boon and Haverkamp, 1982; Boon et al., 1982, 1983b). According to Esteves (1979), floating-leaved macrophytes possess a relatively small cell wall fraction (mean value approximately 42%) compared to several submerged and emergent water plants (with mean values of approximately 48 and 59%, respectively). The relatively fast weight loss and change in organic matter composition of decaying floating-leaved macrophytes can be explained, at least in part, by the relatively low structural carbohydrate levels in the green tissues (see e.g., Godshalk and Wetzel, 1978) and by the rapid loss of the relatively large protoplasmic component of these plants.

The effect of the season

It is important for the further fate of plant material at what time in the season it enters the detrital pool, because of seasonal variations in environmental circumstances and chemical composition of the plant material. Natural senescence of floating leaves of *Nymphaea alba* is a common phenomenon during the entire growing season. According to Van der Velde (1980), the mean leaf persistence of *Nymphaea alba* at the water surface varies between 39 and 46 days in the Oude Waal; the turnover rate of the leaves was estimated to vary between 3.8 and 4.9.

In the present study, considerable differences in the decay patterns of the *Nymphaea* leaves were observed in the Oude Waal between summer and autumn. The faster loss of mass and change in organic matter composition in summer can be explained largely by the higher temperatures and consequently by the higher metabolic activity of the decomposers. In several laboratory studies, the rate of weight loss (Godshalk and Wetzel, 1978; Carpenter and Adams, 1979; De Lyon et al., 1983; Brock, 1984) and the rate of change in organic matter composition of macrophyte material (Godshalk and Wetzel, 1978; Boon et al., 1982, 1983b) have been found to be correlated with temperature. In the Oude Waal, at the end of the incubation periods of both the summer and autumn experiment, an accumulation of lignin components in the particulate residues of the decomposing *Nymphaea* leaves could be demonstrated. In this system, only the decomposition rate and not the route of decomposition was affected by the lower temperatures in autumn.

Besides temperature, other physico-chemical properties of the water,

such as ambient nitrogen and phosphorus concentrations, might have caused some variation in rates of weight loss and compositional change between summer and autumn. Usually, the inorganic nitrogen and phosphorus levels are higher in the overlying water during the colder period of the year. Nevertheless, our data suggest that in the Oude Waal, the effect of seasonal changes in temperature on the decay of *Nymphaea* material is far more important than the effect of seasonal changes in nutrient content of the ambient water.

Not only seasonal changes in the physico-chemical properties of the ambient water (particularly temperature), but also seasonal changes in the chemical composition of the *Nymphaea* leaves explain some of the variation in the rate of decay between different periods of the year. *Nymphaea* leaves harvested in both the Voorste Choorven and the Oude Waal had higher protein levels earlier in the growing season and higher contents of structural carbohydrates later on. The observed differences between Laboratory Experiments III and IV indicate that the rate of weight loss as well as the rate of compositional change is smaller when *Nymphaea* material with a high initial structural carbohydrate content is used. The *Nymphaea* leaves harvested at different times in a particular system also showed variations in elemental composition. Although we observed a stimulation of the weight loss of *Nymphaea* material with a low initial nitrogen content in a medium enriched with nitrate or ammonium, a clear correlation between the initial concentration of nitrogen in the plant material and its decay rate could not be demonstrated. We suppose that in some of our laboratory experiments the metabolic activity of decomposers was limited by nitrogen. In these experiments, larger ambient nitrate or ammonium concentrations compensated for lower nitrogen levels in the *Nymphaea* leaves. Such a phenomenon has also been observed in decomposing *Myriophyllum* (Carpenter and Adams, 1979).

The effect of the trophic status and pH of the medium

In the present study, considerable variations in the loss of mass and the change in organic matter composition of decaying *Nymphaea* leaves were observed between an alkaline, eutrophic oxbow lake (Oude Waal) and an acidified moorland pool (Voorste Choorven). Although we observed some site-dependent differences in the initial chemical composition of the *Nymphaea* leaves, our data clearly indicate that differences in the chemistry of the ambient water of the Oude Waal and Voorste Choorven determine to a greater extent the rate and route of decomposition of the *Nymphaea* material.

In the Oude Waal and in the laboratory, in media enriched with bicarbonate or nitrate-orthophosphate, we observed a relatively high rate of weight loss and a rapid change in organic matter composition of decaying *Nymphaea* leaves. In the laboratory, a relatively high rate of weight loss of

the leaves was also observed in some media enriched with nitrate or ammonium. Apparently, the decay of macrophyte material is faster under more eutrophic and/or alkaline conditions. The decomposition of *Nymphaea* leaves in eutrophic and/or alkaline environments resulted in a loss of the organic molecules associated with the protoplasm and of the cellulose and hemicellulose polymers associated with the cell walls, so that lignin accumulated in the particulate residues.

In the Voorste Choorven (with a pH of approximately 4), and in acid water (pH 3) in the laboratory, a relatively low rate of weight loss and a slow compositional change of decaying *Nymphaea* leaves was found. In these acid environments, we observed the disappearance of the more or less soluble components of the decomposing *Nymphaea* leaves (a phenomenon which can largely be attributed to physical leaching), while the loss of structural carbohydrates and lignin was very small. Carbohydrates rich in pentose (hemicellulose) particularly accumulated in the particulate residues.

Under laboratory conditions, an inhibition of the weight loss of decomposing plant material at lower pH regimes in an aqueous environment is reported for tree-leaf litter (Traaen, 1980), *Carex* litter (McKinley and Vestal, 1982) and *Nymphaea* detritus (this study). Furthermore, in several field studies a slower loss of mass of decomposing plant material was observed in acid waters (Friberg et al., 1980; Hendrey, 1982; Carpenter et al., 1983; Otto and Svensson, 1983; Brock et al., 1985). The slower breakdown in acid-stressed aquatic ecosystems can be attributed to a reduction in microbial biomass and a lower metabolic activity of the decomposer community (Bick and Drews, 1973; McKinley and Vestal, 1982; Rao and Dutka, 1983). Most bacteria can only grow within the range pH 4—9, while the optimum for most aquatic bacteria is between pH 6.5 and 8.5. However, there are more acidophilous fungi than bacteria (Rheinheimer, 1974).

A high bicarbonate concentration in the water was an important decay-stimulating factor in our laboratory experiments. This phenomenon can most probably be attributed to the high buffering capacity of the bicarbonate concentrations employed, although the actual use of the bicarbonate as a nutrient for microorganisms cannot be excluded. In our experiments, the litter bags with *Nymphaea* material were incubated under aerobic conditions, nevertheless, it seems likely that within the particulate matter or accumulated detritus, anaerobic conditions and acid microenvironments were created due to microbial activity. In these acid microenvironments, the activity of the decomposer community is slowed down. However, ambient water with a high bicarbonate concentration, has the capacity to neutralise acid substances. A certain volume of a medium with a high bicarbonate concentration which is transported inside accumulated detritus has a much higher buffering capacity than the same volume of a medium low in bicarbonate and with the same pH. We know no other studies on the loss of mass and the change in organic matter composition of decom-

posing macrophyte detritus in relation to the bicarbonate level of the water.

The literature concerning the effect of nitrogen and/or phosphorus enrichment of the ambient water on the decay of plant material is rather inconsistent and mostly concerns the loss of mass only. It was demonstrated in several laboratory experiments that extra nitrogen in the medium stimulated the loss of mass of aquatic macrophyte detritus (Carpenter and Adams, 1979; this study) and tree-leaf litter (Kaushik and Hynes, 1971; Howarth and Fisher, 1976). However, in various other laboratory experiments, the loss of mass of the same types of detritus was not influenced by inorganic nitrogen enrichment of the ambient medium (Harrison and Mann, 1975; Triska and Sedell, 1976; Federle et al., 1982; this study). A faster loss of mass of decomposing plant material in water enriched with both inorganic nitrogen and phosphorus has been demonstrated for *Nymphaea* detritus (this study) and for *Phragmites* (Polunin, 1982) and tree-leaf litter (Howarth and Fisher, 1976), while a similar treatment had no effect on the weight loss of *Carex* litter (Federle et al., 1982). In nearly all laboratory studies mentioned, a stimulating effect on the weight loss of decomposing plant material by orthophosphate alone could not be demonstrated. The inconsistency of the literature concerning the effect of inorganic nitrogen and/or phosphorus enrichment of the water on the weight loss of decaying macrophytes can be explained largely by the variations in chemical composition of the plant material employed. The growth of microorganisms associated with the detritus can be limited if the nutrient salt contents (e.g., nitrogen) of both the detritus and the ambient water are low. Such a nutrient limitation most probably does not occur when the nutrient salt level of the detritus is high and that of the water low or the other way around (see also discussion above).

Our observation that in the eutrophic water of the Oude Waal and in nitrate-orthophosphate-enriched water in the laboratory the cellulose and hemicellulose polymers were lost from decomposing *Nymphaea* leaves, whereas lignin accumulated in the particulate residues, is in accordance with results presented by Federle and Vestal (1980). These investigators observed a faster mineralization of cellulose of *Pinus* and *Carex* in water enriched with nitrogen and phosphorus. However, the mineralization of the lignins from these plants was inhibited by phosphorus additions to water.

Processes like eutrophication with nitrogen and phosphorus, alkalinisation and acidification strongly influence the rate and route of plant material decomposition in freshwater ecosystems. A stimulation or inhibition of decay processes certainly affects the whole biocoenosis associated with aquatic macrophytes, since the detritus food chain is very important in macrophyte-dominated systems. However, the structure and functioning of the decomposer community associated with floating-leaved macrophytes largely remains to be investigated.

CONCLUSIONS

During the initial decay period of the *Nymphaea* leaves, non-structural carbohydrates, proteinaceous material and phenolic compounds leached out and/or were metabolised at relatively high rates by microorganisms. The rate of disappearance of cellulose, hemicellulose and lignin from the particulate residues was relatively low and depended to a greater extent on the physico-chemical properties of the ambient water.

Differences in decay patterns of the *Nymphaea* leaves were observed between summer and autumn. A faster loss of mass and a higher rate of change in organic matter composition observed in summer is explained largely by the higher temperatures. However, seasonal changes in the chemical composition of the plant material also played a role. In the course of the season, there was a tendency for increased structural carbohydrates and lignin to be present in the fresh *Nymphaea* leaves. Although in the alkaline oxbow lake significantly different decomposition rates were found between summer and autumn, no large differences in the routes of decomposition could be observed. In both summer and autumn, an accumulation of lignin components in the particulate residues could be demonstrated.

Considerable differences in decay patterns of the leaves were observed between the alkaline oxbow lake, the acid moorland pool and some of the media in the laboratory. pH and alkalinity values and nitrogen-phosphorus concentrations of the water particularly influenced the rate and route of decomposition of the *Nymphaea* material. The weight loss and change in organic matter composition of decomposing *Nymphaea* leaves was faster under more eutrophic and/or alkaline conditions. In eutrophic and/or alkaline environments, lignin accumulated in the particulate residues, while other structural carbohydrates such as cellulose and hemicellulose apparently were mineralised. In the acid moorland pool and in acid water in the laboratory, a low rate of weight loss and a slow compositional change of decaying *Nymphaea* leaves was found. In these acid environments, the loss of structural carbohydrates and lignin from the decomposing leaves was small; carbohydrates rich in pentose (hemicellulose) particularly, accumulated in the particulate residues.

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REFERENCES

Bick, H. and Drews, E.F., 1973. Selfpurification and silicate communities in an acid milieu (model experiments). Hydrobiologia, 42: 393—402.

Boon, J.J. and Haverkamp, J., 1982. Pyrolysis mass spectrometry of intact and decomposed leaves of *Nuphar variegatum* and *Zostera marina*, and some archeological eelgrass samples. Hydrobiol. Bull. (Amsterdam), 16: 71—82.

Boon, J.J., Wetzel, R.G. and Godshalk, G.L., 1982. Pyrolysis mass spectrometry of some *Scirpus* species and their decomposition products. Limnol. Oceanogr., 27: 839—848.

Boon, J.J., Eijkel, G.B. and Best, E.P.H., 1983a. Study of the seasonal change in composition in roots and shoots of *Phragmites australis* by pyrolysis mass spectrometry combined with multivariate data analysis. Proc. Int. Symp. Aquat. Macrophytes, 18—23 September 1983, Nijmegen, The Netherlands. pp. 30—34.

Boon, J.J., Windig, W., Wetzel, R.G. and Godshalk, G.L., 1983b. The analytical pyrolysis of particulate residues of decomposing *Myriophyllum heterophyllum*. Aquat. Bot., 15: 307—320.

Brock, Th. C.M., 1984. Aspects of the decomposition of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Aquat. Bot., 19: 131—156.

Brock, Th.C.M., Huijbrechts, C.A.M., Van de Steeg-Huberts, M.J.H.A. and Vlassak, M.A., 1982. In situ studies on the breakdown of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae); some methodological aspects of the litter bag technique. Hydrobiol. Bull. (Amsterdam), 16: 35—49.

Brock, Th.C.M., Bongaerts, M.C.M., Heijnen, G.J.M.A. and Heijthuijsen, J.H.F.G., 1983. Nitrogen and phosphorus accumulation and cycling by *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Aquat. Bot., 17: 189—214.

Brock, Th.C.M., De Lyon, M.J.H., Van Laar, E.M.J.M. and Van Loon, E.M.M., 1985. Field studies on the breakdown of *Nuphar lutea* (L.) Sm. (Nymphaeaceae), and a comparison of three mathematical models for organic weight loss. Aquat. Bot., 21: 1—22.

Carpenter, J., Odum, W.E. and Mills, A., 1983. Leaf litter decomposition in a reservoir affected by acid mine drainage. Oikos, 41: 165—172.

Carpenter, S.R. and Adams, M.S., 1979. Effects of nutrients and temperature on decomposition of *Myriophyllum spicatum* L. in a hard water eutrophic lake. Limnol. Oceanogr., 24: 520—528.

De Lyon, M.J.H., Van Laar, E.M.J.M. and Brock, Th.C.M., 1983. A comparison of three mathematical models for the description of breakdown of *Nuphar lutea* detritus. Proc. Int. Symp. Aquat. Macrophytes, 18—23 September, 1983, Nijmegen, The Netherlands. pp. 129—133.

Esteves, F., 1979. Die Bedeutung der aquatischen Makrophyten für den Stoffhaushalt des Schöhsees. II. Die organischen Haubtbestandteile und der Energiegehalt der aquatischen Makrophyten. Arch. Hydrobiol. Suppl., 57: 144—187.

Federle, T.W. and Vestal, J.R., 1980. Lignocellulose mineralization by arctic lake sediments in response to nutrient manipulation. Appl. Environ. Microbiol., 40: 32—39.

Federle, T.W., McKinley, V.L. and Vestal, J.R., 1982. Effects of nutrient enrichment on the colonization and decomposition of plant detritus by the microbiota of an arctic lake. Can. J. Microbiol., 28: 1199—1205.

Friberg, F., Otto, C. and Svensson, B.S., 1980. Effects of acidification on the dynamics of allochthonous leaf material and benthic invertebrate communities in running waters. In: D. Drabløs and A. Tollan (Editors), Ecological Impact of Acid Precipitation. Proc. Int. Symp. March 1980, Sandefjord, Norway. pp. 304—305.

Godshalk, G.L. and Wetzel, R.G., 1978. Decomposition of aquatic angiosperms. II. Particulate components. Aquat. Bot., 5: 301—327.

Harrison, P.G. and Mann, K.H., 1975. Detritus formation from eelgrass (*Zostera marina*): The relative effects of fragmentation, leaching and decay. Limnol. Oceanogr., 20: 924—934.

Hendrey, G.R., 1982. Effects of acidification on aquatic primary producers and decomposers. In: R.E. Johnson (Editor), Acid Rain/Fisheries. Proc. Int. Symp. on Acidic Precipitation and Fishery Impacts in Northeastern North America, August 2—5, 1981, Ithaca, New York. pp. 125—135.

Hoogerbrugge, R., Willig, S.J. and Kistemaker, P.G., 1983. Discriminant analysis by double stage principal component analysis. Anal. Chem., 55: 1711—1712.

Howarth, R.W. and Fisher, S.G., 1976. Carbon, nitrogen, and phosphorus dynamics during leaf decay in nutrient enriched stream micro-ecosystems. Freshw. Biol., 6: 221—228.

Jenny, H., Gessel, S.P. and Bingham, F.T., 1949. Comparative study of decomposition of organic matter in temperate and tropical regions. Soil Sci., 68: 419—432.

Kaushik, N.K. and Hynes, H.B.N., 1971. The fate of dead leaves that fall into streams. Arch. Hydrobiol., 68: 465—515.

McKinley, V.L. and Vestal, J.R., 1982. Effects of acid on plant litter decomposition in an arctic lake. Appl. Environ. Microbiol., 43: 1188—1195.

Meuzelaar, H.L.C., Kistemaker, P.G., Eshuis, W. and Boerboom, H.A.J., 1977. Automated pyrolysis mass spectrometry; application to the differentiation of microorganisms. In: N.R. Daly (Editor), Advances in Mass Spectrometry, Vol. 7B. Heyden, London, pp. 452—456.

Meuzelaar, H.L.C., Haverkamp, J. and Hileman, F.D., 1982. Pyrolysis Mass Spectrometry of Recent and Fossil Biomaterials. Elsevier, Amsterdam, 293 pp.

Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology, 44: 322—331.

Otto, C. and Svensson, B.S., 1983. Properties of acid brown water streams in South Sweden. Arch. Hydrobiol., 99: 15—36.

Polunin, N.V.C., 1982. Processes contributing to the decay of reed (*Phragmites australis*) litter in fresh water. Arch. Hydrobiol., 94: 182—209.

Rao, S.S. and Dutka, B.J., 1983. Influence of acid precipitation on bacterial populations in lakes. Hydrobiologia, 98: 153—157.

Rheinheimer, G., 1974. Aquatic Microbiology. Wiley, New York, 184 pp.

Roelofs, J.G.M., 1983. Impact of acidification and eutrophication on macrophyte communities in soft waters in The Netherlands. I. Field observations. Aquat. Bot., 17: 139—155.

Roelofs, J.G.M., Schuurkes, J.A.A.R., and Smits, A.J.M., 1984. Impact of acidification and eutrophication on macrophyte communities in soft waters. II. Experimental studies. Aquat. Bot., 18: 398—411.

Rogers, K.H. and Breen, C.M., 1982. Decomposition of *Potamogeton crispus* L.: the effects of drying on the patterns of mass and nutrient loss. Aquat. Bot., 12: 1—12.

Saiz-Jimenez, C. and De Leeuw, J.W., 1985. Pyrolysis gas chromatography mass spectrometry of isolated, synthetic and degraded lignins. Organ. Geochem., 6: 417—423.

Scheffé, H., 1959. The Analysis of Variance. A Wiley Publication in Mathematical Statistics. Wiley, New York, 477 pp.

Thimann, K.V., 1978. Senescence. Bot. Mag. Tokyo, Spec. Iss. 1: 19—43.

Traaen, T.S., 1980. Effects of acidity on decomposition of organic matter in aquatic environments. In: D. Drablφs and A. Tollan (Editors), Ecological Impact of Acid Precipitation. Proc. Int. Symp., March 1980, Sandefjord, Norway. pp. 340—341.

Triska, F.J. and Sedell, J.R., 1976. Decomposition of four species of leaf litter in response to nitrate manipulation. Ecology, 57: 783—792.

Van der Kaaden, A., Haverkamp, J., Boon, J.J., and De Leeuw, J.W., 1983. Analytical pyrolysis of carbohydrates. I. Chemical interpretation of matrix influences on pyrolysis-mass spectra of amylose using pyrolysis-gas chromatography-mass spectrometry. J. Anal. Appl. Pyrol., 5: 199—220.

Van der Velde, G., 1980. Studies in nymphaeid-dominated systems with special emphasis on those dominated by *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Thesis Nijmegen, Stichting Studentenpers Nijmegen, The Netherlands, 163 pp.

Van der Velde, G. and Peelen-Bexkens, P.M.M., 1983. Production and biomass of floating leaves of three species of Nymphaeaceae in two Dutch waters. Proc. Int. Symp. Aquat. Macrophytes, 18—23 September, 1983, Nijmegen, The Netherlands. pp. 230—235.

Windig, W., Kistemaker, P.G. and Haverkamp, J., 1981. Chemical interpretation of differences in pyrolysis-mass spectra of simulated mixtures of biopolymers by factor analysis with graphical rotation. J. Anal. Appl. Pyrol., 3: 199—212.

Windig, W., Haverkamp, J. and Kistemaker, P.G., 1983. Interpretation of sets of pyrolysis mass spectra by discriminant analysis and graphical rotation. Anal. Chem., 55: 81—87.

THE ECOLOGICAL ROLE OF THE WHITE, YELLOW AND FRINGED WATERLILY A SYNTHESIS

Introduction.

The occurrence of dense stands of *Nuphar lutea* (L.)Sm., *Nymphaea alba* L. and *Nymphoides peltata* (Gmel.)O Kuntze is dependent on a variety of more or less specific chemical and physical habitat factors (Chapter 2). But the relation between a nymphaeid vegetation and its surroundings works two ways in that nymphaeids influence several physico-chemical properties of their environment by their characteristic architecture, their metabolic activities and by products arising from their decomposition. The physical framework of the nymphaeid vegetation and the specific physico-chemical conditions prevalent in waterlily beds give rise to more or less suitable circumstances for other organisms.

In this chapter the effects of dense stands of nymphaeid water plants on some important physical and chemical properties of their surroundings are reviewed In addition, the opportunities and constraints which the nymphaeid vegetation provides for other organisms are discussed.

Biomass.

In eutrophic ecosystems in The Netherlands *Nuphar lutea, Nymphaea alba* and *Nymphoides peltata* usually have an aboveground biomass not exceeding ca. 300-350 g ash-free dry weight per m^2 (Table I). The characteristic architecture of nymphaeids, with the leaves floating in what is essentially a single layer on the surface of the water, limits the potential aboveground biomass of these water plants. Nevertheless, their total peak biomass can be considerably higher due to a well-developed root-stock system. In the Oude Waal, a total peak biomass of more than 1 kg ash-free dry weight per m^2 macrophyte stand was recorded for *Nymphaea alba* (Table I).

Table I.
Peak biomass values (Bmax) of aboveground and total *Nuphar lutea*, *Nymphaea alba* and *Nymphoides peltata* as found in some eutrophic waters in The Netherlands and expressed in g ash-free dry weight per m^2 macrophyte stand.

Species System	Aboveground Bmax mean sd	Total Bmax mean sd	Source
Nuphar lutea			
Oude Waal	203 ± 57 (n=5)	418 ± 154 (n=5)	a, b, c
Haarsteegse Wiel	338 (n=1)	-	b, d
Broekse Wielen	267 (n=1)	-	e
Nymphaea alba			
Oude Waal	268 ± 23 (n=3)	1088 ± 317 (n=3)	b, c, f
Nymphoides peltata			
Bemmelse Strang	277 ± 29 (n=4)	372 ± 38 (n=4)	g

(a) Vintges and Verhoeven, 1977.
(b) Van der Velde and Peelen-Bexkens, 1983.
(c) Brock and Van der Velde, unpublished.
(d) Stemkens and Meekes, 1980.
(e) Clasquin and Crul, 1982.
(f) Ankersmid and Kwak, 1979.
(g) chapter 3.

Table II.
Estimates of the annual organic matter production per m^2 macrophyte stand (in g ash-free dry weight) and the P/Bmax ratio of aboveground *Nuphar lutea*, *Nymphaea alba* and *Nymphoides peltata* in some eutrophic aquatic ecosystems.

Species System	Aboveground production	P/Bmax	Source
Nuphar lutea			
Oude Waal	557	2.74	a
Haarsteegse Wiel	862	2.55	a
Nymphaea alba			
Oude Waal	749	2.79	a
Nymphoides peltata			
Bemmelse Strang	969	3.50	b

(a) calculated after Van der Velde and Peelen-Bexkens, 1983.
(b) chapter 3.

Production.

Due to the high turn-over rates of the floating leaves the annual organic matter production (=P) of the aboveground parts is much higher than the recorded aboveground peak biomass values. The estimated P/Bmax ratios of aboveground *Nuphar lutea* and *Nymphaea alba* are more or less of the same magnitude, while that of *Nymphoides peltata* is considerably higher (Table II). In the Oude Waal, Haarsteegse Wiel and Bemmelse Strang the annual organic matter production by the aboveground parts of nymphaeids varied between 557 and 969 g ash-free dry weight per m^2 macrophyte stand (Table II). The aboveground parts of *Nuphar, Nymphaea* (Esteves, 1979) and *Nymphoides* (Kaul, 1971) show relatively high contents of crude protein, crude fat and non-structural carbohydrates, while their cell wall fraction is relatively low Therefore, the organic matter produced by the aboveground parts constitutes a good food and energy source for other organisms, both quantitatively and qualitatively.

Compared to the information which is available concerning the aboveground parts of *Nuphar lutea, Nymphaea alba* and *Nymphoides peltata*, relatively little is known about the organic matter produced annually by the underground parts. In the Bemmelse Strang the root-stock system of *Nymphoides peltata* contributed ca. 7% to the total production (see Chapter 3). Preliminary studies on the underground parts of *Nuphar* and *Nymphaea* in the Oude Waal have revealed that their roots and root-stocks contributed ca. 10-20% to the total organic matter production of these plants (Vintges and Verhoeven, 1977; Ankersmid and Kwak, 1978).

The fate of the organic matter produced.

The flow of organic matter from nymphaeids to other trophic levels takes place by secretion, by direct herbivore grazing and by decomposition of senescent and dead plant parts.

Secretion.

Secretion of organic matter occurs e.g. in the floral parts. The flowers of *Nymphoides peltata* and *Nuphar lutea* secrete nectar and those of *Nymphaea alba* stigmatic exudate. Although the amounts of nectar and stigmatic exudate secreted are very small compared to the total organic matter production of the nymphaeids, these products may be important for various

flower-visiting insects (Van der Velde et al., 1978, Van der Velde and Van der Heijden, 1981). The flowers of *Nuphar* and *Nymphaea* supply the main source of food for the adult stage of the nymphaeid-associated fly *Notiphila brunnipes* R.-D. (Van der Velde and Brock, 1980).

The secretion of dissolved organic matter by the intact leaves and underground parts of *Nuphar, Nymphaea* and *Nymphoides* has not been measured. Generally, the organic matter losses from aquatic macrophytes due to secretion constitute only a few per cent of the total organic matter production, although sometimes it may be over 20% of the fixed carbon (e.g. Wetzel and Manny, 1972; Søndergaard, 1981). The dissolved organic matter released by intact macrophytes may be directly utilized by epiphytic and planktonic organisms (Allen, 1971; Blindow, 1984).

Grazer food-chain

The importance of *Nuphar lutea, Nymphaea alba* and *Nymphoides peltata* for herbivores is well documented. Gaevskaya (1966) and Van der Velde (1980) have shown that most herbivores of nymphaeids are terrestrial or semi-aquatic organisms; of the animals which complete their whole life-cycle in the water, relatively few are able to consume the living tissues of these plants. Consumption by animals takes place on a large scale, as large parts of the nymphaeid vegetation are removed by e.g. cows or muskrats (Heine and Van der Velde, 1978), as well as on a small scale, where only fragments of plant parts are consumed by e.g. herbivorous insects (Lammens and Van der Velde, 1978). Consumption of nymphaeid vegetation on a large scale is a very local phenomenon, while consumption on a microscale can be observed almost everywhere.

Most herbivorous insects of nymphaeids show a preference for the young floating leaves. The herbivores probably find more nutritive food in young plant parts (Van der Velde and Van der Heijden, 1985; Van der Velde and Hiddink, submitted).

Van der Velde et al. (1982) have attempted to measure the amount of nymphaeid material consumed by herbivores. They found that these animals were responsible for the disappearance of ca. 22% of the leaf area produced annually by *Nymphoides peltata*. This percentage is, however, the combined effect of consumption and damage succeeded by microbial decay. Actual grazing can be estimated to take away no more than ca. 10% of the production of

leaf-blades. Since most herbivores consume the leaf-blades in particular it can be assumed that probably no more than 5% of the total organic matter produced by *Nymphoides peltata* enters the grazer food-chain. Observations in the field suggest that similar amounts of plant material are grazed from *Nuphar lutea* and *Nymphaea alba*.

Although in nymphaeid systems the amount of macrophyte material which enters the grazer food-chain is relatively small, this fraction is very important for certain associated animals. Some herbivorous insects of nymphaeids are host-specific and are thus completely dependent on these water plants. Some examples of herbivorous insects which graze exclusively on nymphaeids are the fly *Hydromyza livens* (F.), which completes its life cycle on some *Nuphar* species (Brock and Van der Velde, 1983), and the beetles *Donacia crassipes* (F.) and *Pyrrhalta nymphaea* (L.) f. *typica*, which feed on both *Nymphaea* and *Nuphar* (Van der Velde, 1980).

Detritus food-chain

The major part of the organic matter produced annually by nymphaeids enters the detritus food-chain. Bacteria and fungi can be regarded as the most important decomposers. Although several more or less characteristic fungi were isolated from decomposing leaves of nymphaeids (Lammens and Van der Velde, 1978; Van der Aa, 1978; Jacobs, 1982), results presented in chapter 5 suggest that bacteria play a more important role in the mineralization of nymphaeid material than fungi, at least in eutrophic alkaline water. The relative contributions of bacteria and fungi, however, may be strongly dependent on the physico-chemical properties of the habitat (e.g. pH). Generally, very little information is available on the taxonomic status of the micro-organisms which perform the mineralization of nymphaeid material. The fact that some pythiaceous fungi new for The Netherlands were isolated from decomposing *Nymphoides* leaves (Jacobs, 1982) may indicate that certain micro-organisms are restricted to the detritus from nymphaeids, but this result might just as well find its explanation in the poor knowledge of the communities of micro-organisms present in shallow freshwater habitats.

Micro-organisms which colonize plant detritus increase its nutritive value (e.g. Barlocher and Kendrick, 1975), at least in certain stages of the decomposition process. The number of macro-invertebrate individuals on nymphaeid detritus is most

probably highest when this material is fully conditioned by micro-organisms. After a decomposition process of 42 days in the Oude Waal more than 800 macro-invertebrate individuals (with a total ash-free dry weight of 570 mg) were found per g ash-free dry weight of *Nymphaea* detritus (Table III). In the oxbow lake environment comparable amounts were found on detritus of *Nuphar lutea* and *Nymphoides peltata* (see e.g. Chapter 5). Not only detritivorous animals colonize the detritus of nymphaeids but also carnivorous macro-invertebrates such as leeches, triclads and water mites. The detritivores in and on detritus are suitable prey organisms for carnivores. Generally, the macro-invertebrates present in and on detritus from nymphaeids are not typical for the nymphaeid system. These animals can also be found on other types of detritus.

Table III.
The number of taxa and individuals and the biomass (in mg ash-free dry weight) of macro-invertebrates found per g ash-free dry weight detritus of leaf-blades of *Nymphaea alba* in the course of its decomposition in litter bags in the Oude Waal during the summer of 1983.

Incubation period (days)	7	14	28	42	62
Number of taxa	19	21	23	29	28
Number of individuals/g	11	43	353	814	273
mg macro-invertebrates/g	11	36	173	570	281

In eutrophic, alkaline ecosystems such as the Oude Waal and Bemmelse Strang the activities of the decomposer community result in the disappearance of ca. 70-95% of the coarse detritus from aboveground parts of *Nuphar, Nymphaea* and *Nymphoides* within 1-3 months (Chapters 5, 6 and 7). The remaining fraction accumulates in the sediment where it decomposes very slowly. In eutrophic, alkaline water an accumulation of lignin components in the particulate residues was demonstrated (Chapter 7). The amount and chemical composition of the refractory detritus from nymphaeids, which accumulates more or less permanently in the sediment, is highly dependent on the trophic status of the system. In acid environments a larger fraction remains, which turns into a more or less permanent sediment, and under these circumstances an accumulation of structural carbohydrates (particularly hemicellulose) in the particulate residues was demonstrated (Chapter 7).

Dense stands of nymphaeids contribute to the formation of a sapropel layer on the bottom and thus strongly influence the physico-chemical properties of the sediment. Due to the sedimentation of refractory organic matter the water becomes shallower, which ultimately results in a succession towards a marsh vegetation.

Nutrient accumulation and cycling.

Plants take up nutrients such as inorganic nitrogen and phosphorus from their ambient environment and store them in their tissues. The amounts of nitrogen and phosphorus stored in nymphaeids per m^2 macrophyte stand may be relatively large (Table IV), certainly in comparison with the N and P present in the overlying and interstitial water (Chapter 4).

Table IV.
Maximum amounts of nitrogen (N) and phosphorus (P) stored in aboveground and total *Nuphar lutea*, *Nymphaea alba* and *Nymphoides peltata* as found in some eutrophic waters in The Netherlands and expressed in mmol per m^2 macrophyte stand.

Species System	Aboveground N	 P	Total Biomass N	 P	Source
Nuphar lutea					
Oude Waal	237	33.6	347	63.6	a, b
Haarsteegse Wiel	265	33.7	-	-	a, b
Broekse Wielen	461	30.5	-	-	c
Nymphaea alba					
Oude Waal	302	31.3	843	175.5	a, b
Nymphoides peltata					
Bemmelse Strang	266	47.4	334	56.6	d

(a) Roelofs, unpublished.
(b) biomass data Table I.
(c) Clasquin and Crul, 1982.
(d) chapter 4.

The interstitial water is the most important source of inorganic N and P for nymphaeids. In these macrophytes nutrient translocation from the sediments to the roots and from the underground to the aboveground parts is facilitated by evapotranspiration by the floating leaves. Twilley et al. (1977) demonstrated that under field conditions roots of *Nuphar* had a greater capacity for the absorption of inorganic P than submerged leaves, while the uptake by floating leaves was negligible. Furthermore, they found a bidirectional flux of P

between submerged leaves and roots and observed that both these organs supplied phosphorus to the floating leaves. Applying a model presented by Carignan (1982) it can be calculated that in the study of Twilley et al. (1977) *Nuphar* absorbed ca. 73% of its inorganic phosphorus needs from the sediments and that in the Bemmelse Strang ca. 80% of the P uptake by *Nymphoides* occurred via the roots (Chapter 4).

Nymphaeids not only store nitrogen and phosphorus but also supply these nutrients to their surroundings. Although nutrient release from intact plant parts may occur (Twilley et al., 1977), the flux of N and P from nymphaeids to the ambient environment takes place largely via the decomposition of aboveground parts. Decomposing leaves of nymphaeids show a rapid nitrogen and phosphorus release (Chapters 5 and 6) and a relatively fast net conversion of organically bound N and P to inorganic forms (Chapter 4). In the oxbow lake environment losses of aboveground biomass of nymphaeids are more or less continuous during the growing season, because of the high turn-over rates of the leaves. In this way nymphaeids act as nutrient pumps between sediment and water during most of the growing season. The amounts of N and P cycled annually by *Nuphar lutea, Nymphaea alba* and *Nymphoides peltata* may be several times larger than the maximum amounts stored in the aboveground parts of these plants (see e.g. Chapter 4).

The released N and P is of importance for planktonic and periphytic algae. In the Oude Waal, Roijackers (1984) observed a higher average fresh weight of phytoplankton in dense nymphaeid stands than in open water, which can be partly explained by the nutrient release from decaying macrophytes. However, the possibility cannot be excluded that under certain circumstances dense stands of nymphaeids compete more or less efficiently with planktonic and epiphytic algae for nutrients in the overlying water, particularly in places where (and periods when) *Nuphar lutea* shows high densities of submerged leaves.

Effects on water movements.

Wave action is reduced by a well-developed floating-leaf canopy. In a nymphaeid vegetation this may result in a somewhat lower aeration and allow a more pronounced thermal stratification of the upper water layers than in comparable places without macrophytes.

Besides diminishing the turbulence at the water surface nymphaeids also reduce the flow of water beneath the floating-leaf canopy. Results presented by Pitlo (1979) indicate that the extent of obstruction is dependent on the nymphaeid species and on its density. A vegetation of *Nuphar lutea*, which may have many submerged leaves, leads to a greater obstruction than e.g. stands of *Nymphaea alba*. The exchange of water (and nutrients) between narrow belts of nymphaeid vegetation and open water is probably not greatly hindered (see e.g. Chapter 4), while large stands of nymphaeids may hamper the flow of water to a larger extent. Generally, a nymphaeid vegetation occupies a relatively small volume of the water column so that its resistance to water flow is usually less pronounced than the obstruction caused by dense stands of submerged macrophytes.

Because of the reduced water movements in and around their stands, nymphaeids may increase sedimentation and trap drifting material (e.g. dead leaves). The root stock systems of these plants also stabilize the sediment so that the water in nymphaeid stands may generally be clearer than that in open water sites. By reducing water movements and by stabilizing the bottom, nymphaeids provide better circumstances for several other organisms. The more or less sheltered circumstances allow the occurrence of e.g. neustonic fauna, insects on the upper sides of the floating leaves, and plants which float at the water surface, such as *Lemna minor* L.. Furthermore, sessile and less mobile aquatic organisms are washed away less easily in dense nymphaeid stands than in open water.

Effects on the oxygen balance.

Daytime photosynthesis and respiration at night by macrophytes with floating leaves do not affect the oxygen concentration of the water as much as do fully submerged macrophytes (see e.g. Kunii, 1983). Oxygen (and carbon dioxide as well) can be exchanged directly with the atmosphere via the stomata at the upper side of the floating leaves. Furthermore, the exchange of gases between nymphaeids and the atmosphere may be facilitated by a flow-through ventilation system as described by Dacey (1981) and Dacey and Klug (1982).

Generally speaking, fully grown nymphaeids have a negative effect on the oxygen balance of the ambient water. Their

photosynthetic oxygen supply to the ambient water is relatively low, their floating leaves reduce gaseous exchanges across the water surface, and oxygen from the water is used when they decompose. Therefore, the water between nymphaeids usually has a somewhat lower oxygen content than that in comparable open water sites (Table V). Nevertheless, the oxygen concentration in the water between nymphaeids is usually high enough to support animal life, because oxygen is supplied by e.g. planktonic and periphytic algae. Furthermore, oxygen-rich water from elsewhere may be transported fairly easily into dense stands of nymphaeids because of their relatively low resistance to the flow of the water.

Table V.
Depth profiles of oxygen content and temperature in the water column of a stand dominated by *Nuphar lutea* (N) and of a moderately exposed open water site (O) in the Oude Waal on a windy sunny day in August.

Depth	% Oxygen saturation		Temperature ^{0}C	
	O	N	O	N
5 cm	100 %	78 %	17.6	19.2
10 cm	-	-	17.6	19.0
20 cm	92 %	79 %	17.3	18.1
30 cm	-	-	17.3	17.9
50 cm	82 %	77 %	17.3	17.6
100 cm	80 %	74 %	17.0	17.2
150 cm	75 %	45 %	16.7	16.9

Gas movements in intercellular spaces of nymphaeids, as described by Dacey (1981), may allow some oxygen release from underground plant parts. Although oxygen release by roots of *Nuphar lutea, Nymphaea alba* and *Nymphoides peltata* remains an important topic for further research, oxidation of the rhizosphere is suggested by the occurrence of ferric hydroxides on the surfaces of the roots. The oxidation of the rhizosphere is considered ecologically important because it may counter the toxicity of reducing compounds in the sediment and alter nutrient availability (Sand-Jensen et al., 1982). Furthermore, by oxidizing the sediment immediately surrounding the roots, nymphaeids may create a favourable environment for several bottom-dwelling organisms. The oxygen present in the intercellular spaces of nymphaeids is also directly exploited by some insects which insert their stigmata into the roots. Larvae and pupae of the beetle *Donacia crassipes* obtain oxygen from the roots of *Nuphar* and *Nymphaea* in this way (Van der Velde, 1980).

The larvae and pupae of the fly *Notiphila brunnipes* (Van der Velde and Brock, 1980) and those of the beetle *Macroplea appendiculata* (Panzer) were found with their stigmata piercing the roots of *Nymphoides peltata*.

Effects on temperature.

Because of their physical construction, nymphaeids convert radiant energy into heat. On sunny days the temperature in the flowers and on the upper surfaces of the floating leaves of *Nuphar lutea* and *Nymphaea alba* may be up to 5°C higher than that of the ambient air (Van der Velde and Brock, 1980; Brock and Van der Velde, 1983). Higher temperatures most probably increase the evapotranspiration by the floating leaves. Willmer (1982) observed that during the day the air just above the floating leaves of *Nymphaea alba* was always more humid than the air just above the water surface, while during the night the air above the floating leaves was often a little drier. According to Willmer (1982) the timing of insect activity on the leaves is related to hygrothermal properties of the microclimate of the upper side of the floating leaves. High temperatures in the flowers are favourable for flower-visiting insects and for the development of the eggs of *Notiphila brunnipes* into larvae (Van der Velde and Brock, 1980).

The capacity of nymphaeids for the conversion of radiant energy into heat not only affects the temperature of the air but also that of the water. The characteristic architecture of nymphaeids is responsible for the fact that particularly the upper water layers are warmed up (Table V). According to Marshall and Westlake (1978), floating-leaved plants may raise the temperature of the water surface by 4-11°C on sunny days, while the mean temperature of the whole water column may be lowered. In macrophyte stands the diurnal fluctuations of temperature are usually higher near the water surface than near the base of the water column (Dale and Gillispie, 1976). The metabolism of the organisms present in a nymphaeid vegetation is certainly influenced by the vertical distribution and diurnal fluctuations of temperature. The higher temperatures near the water surface partly explain why the undersides of the floating leaves are favourable oviposition sites for both aquatic and semi-aquatic animals.

Light interception.

Floating leaves of nymphaeids intercept light and shade the water column (e.g. Makirinta, 1978; Van der Velde, 1980; Roijackers, 1983). By this shading of the water column nymphaeids affect the growth of other plants such as submerged macrophytes, periphytic algae and phytoplankton. The fact that *Nuphar lutea, Nymphaea alba* and *Nymphoides peltata* maintain a vigorous competition for light constitutes one of the reasons why they often occur in monospecific stands in backwaters of the river Waal. In a ditch, Pitlo (1979) observed a reduction in the coverage of submerged macrophytes in the period when high densities of floating leaves were present, a phenomenon which can most probably be attributed to competition for light. The relatively low resistance to the water flow presented by certain nymphaeids, and their capacity to suppress a high biomass of submerged macrophytes, may allow the use of these nymphaeids as a biological control-method for maintaining both the conveyance function and the landscape-ecological function of certain water courses (Zonderwijk and Van Zon, 1976; Pitlo, 1978). The effects of light interception on planktonic and periphytic algae will be treated in detail in the dissertations of Mr. R.M.M. Roijackers and Mr. E.J.P. Delbecque.

Shading the water column also affects the fauna. Darker conditions favour the occurrence of negatively phototactic animals such as flatworms and leeches (Van der Velde, 1980). Furthermore, low light intensities underneath a floating-leaf canopy may make certain animals less vulnerable to predation by fish and birds. Timms and Moss (1984) observed that some large-bodied cladocerans stayed in the nymphaeid vegetation during the day and moved towards open water during twilight. They postulated that during the day these cladocerans were less vulnerable to fish predation in weed beds. Thus, nymphaeid vegetations have an important refuge function for other organisms.

Other physical effects of nymphaeids.

The mere presence of *Nuphar lutea, Nymphaea alba* and *Nymphoides peltata* provides a base for other organisms. For the air-adapted fauna the floating leaves form a flat extension of the littoral border (Van der Velde, 1980). Dense stands of nymphaeids also

provide several m^2 of plant surface area that is used as a substratum by many aquatic organisms (Table VI). In aquatic ecosystems with soft bottoms the availability of a more or less rigid substratum may be a limiting factor for the occurrence of many sessile and/or less mobile organisms. Therefore, the substratum function of aquatic macrophytes is very important for micro-organisms, algae and invertebrates.

Table VI.
The maximum plant surface area in m^2 per m^2 nymphaeid stand available as a substratum for aquatic organisms in the Oude Waal and/or Bemmelse Strang.

Species Location	Area
Nuphar lutea	
Oude Waal	5.2
Bemmelse Strang	3.4
Nymphaea alba	
Oude Waal	3.5
Nymphoides peltata	
Bemmelse Strang	6.1

Because of their position in the air, water and bottom, nymphaeid water plants also contribute to the ecological infrastructure. Many semi-aquatic insects of which the adult stages are air-adapted and of which the larvae live in water use nymphaeid water plants as connecting paths between the different media. Thus the adult insects often deposit their eggs on the undersides of the floating leaves and, just before or after the change from larval stage to adult, they use the floating leaves or peduncles of nymphaeids to crawl out of the water. Without the support of the physical structure of macrophytes the surface tension of the water may be a difficult barrier to pass for semi-aquatic insects. Furthermore, according to Wetzel (1975), the surface tension of the water may be reduced by about 20-30% in places where floating leaves are abundant, facilitating the movements of insects from air to water and vice versa.

Significance for associated organisms.

Nymphaeid water plants are important for other organisms, which are adapted to the physical and chemical conditions discussed earlier, for the following reasons:

a) direct food source for herbivores and for flower-visiting insects which consume nectar, pollen and/or stigmatic exudate,
b) indirect energy and food source for the organisms associated with the detritus food chain,
c) source of mineral salts for periphytic and planktonic algae,
d) source of oxygen for bottom-dwelling organisms (e.g. some insect larvae which insert their stigmata into roots) and for insect larvae which mine the leaves,
e) substratum for periphytic micro-organisms and algae,
f) suitable site/substratum for periphyton-grazing and filter-feeding invertebrates,
g) connecting paths between air, water and bottom for semi-aquatic insects,
h) suitable site/substratum for oviposition by aquatic and semi-aquatic animals,
i) suitable site/substratum for metamorphosis of semi-aquatic insects,
j) hunting ground and territory for mobile terrestrial and aquatic carnivores (e.g. birds, fish and dragonflies),
k) refuge for animals which are vulnerable to predation in open air or open water,
l) shelter against unfavourable weather conditions (e.g. insects which use flowers and/or undersides of aerial leaves to protect themselves against rain),
m) resting and sunning site for animals (e.g. flies which use the flowers to warm up),
n) drinking site for terrestrial and adult semi-aquatic insects (they may use a floating leaf as a platform to drink water),
o) building material for animals in the construction of nests (e.g. for birds such as Grebes) or cases (e.g. the caterpillar *Nymphula nymphaeata* (L.)), and,
p) site of "anchorage" for plants and animals which are vulnerable to wave action, water flow and sediment movement.

For the reasons mentioned above, a nymphaeid vegetation usually harbours more species of algae and invertebrates than comparable sites without macrophytes. In the Bemmelse Strang, an inventory was made of the algae and aquatic invertebrates (including the larval stages of semi-aquatic insects) occurring in stands of *Nymphoides peltata* and in open water sites (Table VII). In all, 459 taxa of algae and invertebrates were found in the *Nymphoides* stands, while in the bare sediment and water

Table VII.
Total number of taxa of algae and aquatic invertebrates (including the larval stages of semi-aquatic insects) found in stands of *Nymphoides peltata* and open water sites in the Bemmelse Strang from 1980-1983. The table is compiled from data presented by Leemans (1982), Geelen et al. (1980), Leuven and Dederen (1981), Van Gool (1982), Van Gool et al. (1982), Dederen et al. (1982) and from the author's personal observations.

	Nymphoides	Open water
ALGAE		
Cyanophyceae	13	11
Xanthophyceae	3	3
Chrysophyceae	10	11
Bacillariophyceae	93	41
Euglenophyceae	14	14
Dinophyceae	3	3
Cryptophyceae	3	3
Chlorophyceae	77	70
Oedogoniophyceae	1	-
Conjugatophyceae	14	7
	231	163
INVERTEBRATES		
Rhizopoda	6	4
Ciliata	18	15
Actinopoda	1	1
Hydrozoa	1	1
Ectoprocta	2	-
Turbellaria	5	1
Rotatoria	32	27
Nematodes	2	2
Oligochaeta	8	7
Hirudinea	8	4
Gastropoda	15	2
Lamellibranchiata	5	-
Ostracoda	6	4
Cladocera	32	17
Copepoda	18	8
Isopoda	1	-
Hydracarina	5	2
Araneae	1	-
Ephemeroptera	3	2
Odonata	3	1
Heteroptera	4	1
Coleoptera	2	-
Megaloptera	1	-
Nematocera	37	18
Brachycera	2	1
Trichoptera	9	3
Lepidoptera	1	-
	228	121

column of open water sites only 284 taxa were observed Of the algae, diatom species (Bacillariophyceae) in particular were more abundant in the *Nymphoides* stand. Generally, diatoms dominate the periphytic community of floating leaves (see e.g. Van der Velde, 1980; Delbecque, 1983). Of the aquatic invertebrates, the Gastropoda, Cladocera, Copepoda and Nematocera in particular showed a higher species richness in the *Nymphoides* vegetation than in open water

The adult stages of insects and spiders occurring in the flowers and on the leaves of *Nymphoides peltata* were investigated in the Oude Waal (Table VIII). In all, 66 insect taxa and 3 spider species were found here on the aerial parts of the Fringed waterlily. Members of the Brachycera were particularly common. Most of the insects and spiders found on the leaves and in the flowers need a more or less solid substratum to rest on and are consequently observed only rarely at the water surface of open water sites.

Table VIII.
Number of insect and spider taxa found by Brock (1975) and Van der Velde and Van der Heijden (1981) on the aerial parts of *Nymphoides peltata* in the Oude Waal.

	Leaves	Flowers	Total
Araneae	3	1	3
Ephemeroptera	4	-	4
Odonata	4	3	4
Hemiptera	-	1	1
Heteroptera	2	-	2
Coleoptera	2	3	4
Nematocera	9	1	9
Brachycera	10	23	26
Hymenoptera	-	4	4
Trichoptera	8	1	8
Lepidoptera	1	4	4
	43	41	69

Besides differences in numbers of species distinct differences between the *Nymphoides* stands and open water sites were also observed in the population densities of associated organisms, particularly in the densities and biomass of aquatic macro-invertebrates. In the *Nymphoides* stands the numbers of individuals and the biomass of macro-invertebrates were considerably higher than in the bare sediment and water column of open water sites (Table IX).

Table IX.
Mean number of individuals and mean biomass (in mg ash-free dry weight) of aquatic macro-invertebrates per m^2 of macrophyte stans occurring on the macrophyte, in the sediment and in the water column of sites with *Nymphoides peltata* and of open water sites in the Bemmelse Strang in 1982.

	Nymphoides stand		Open water site	
	numbers	biomass	numbers	biomass
Macrophyte	1064	240	-	-
Sediment	3656	6220	2611	542
Water column	97	13	19	3

Most organisms found in association with nymphaeid vegetation are not intrinsically bound to the nymphaeid system, since they occur in other habitats as well (Van der Velde, 1980). Certain species combinations, however, are very typical for the nymphaeid system (e.g. Van der Velde et al., accepted). Some characteristic organisms of nymphaeid vegetation in The Netherlands are the parasitic fungi *Colletotrichum nymphaeae* (Pass)van der Aa (Van der Aa, 1978) and *Septoria villarsiae* Desm. (Lammens and Van der Velde, 1978), the chironomid *Endochironomus lepidus* (Meigen) (Van der Velde and Hiddink, submitted), the flies *Hydromyza livens* (Brock and Van der Velde, 1983), *Notiphila brunnipes* (Van der Velde and Brock, 1980), *Notiphila dorsata* Stenh., *Spatiophora hydromyzina* Fall., *Dolichopus latilimbatus* (Macq.), *Campsicnemus picticornis* (Zett.) and *Rhaphium antennatum* (Carl.), the aphid *Rhopalosiphum nymphaeae* (L.), the bug *Mesovelia furcata* Mulsant et Rey, the beetles *Donacia crassipes* and *Pyrrhalta nymphaeae* f. *typica* and the dragonfly *Erythromma najas* (Hansemann) (Van der Velde, 1980). It is noteworthy that all these characteristic organisms are adapted to the air, at least during a part of their life cycle.

Relations with surrounding habitats.

Aquatic ecosystems can be regarded as a nutrient trap for the surrounding terrestrial systems. Organic matter and nutrients of terrestrial origin are trapped and processed in the littoral macrophyte beds. Also, many of the organisms that can be found in nymphaeid vegetation occur, in one or more stages of

their development, in terrestrial habitats. Dolichopodid flies are inhabitants of the nymphaeid system in their adult stage only (see e.g. Van der Velde et al., accepted). Many semi-aquatic insects such as Nematocera and Odonata spend their larval life in nymphaeid vegetation, while their mature stages have predominantly a terrestrial mode of life. The migration of adult semi-aquatic insects to terrestrial habitats may constitute an important loss of organic matter and nutrients from shallow aquatic ecosystems. Nymphaeid water plants are also dependent on the activities of terrestrial organisms. Ordinary terrestrial insects such as honeybees and bumblebees are the most important pollinators of the Yellow and Fringed waterlily (see e.g. Brock, 1975). In addition, the dispersal of their seeds to other aquatic systems may depend on activities of animals with a more or less terrestrial mode of life.

Within the same aquatic ecosystem many interrelations between nymphaeid vegetation and other habitats can be recognized. The organic matter produced and the nutrients released by nymphaeid water plants are partly transported to surrounding habitats, particularly to deeper open water sites. Oxygen-rich water from the open water can be transported into nymphaeid vegetation. Birds that brood in the shelter of the reed belt may use the nymphaeid vegetation for foraging purposes. Different stages of the life cycles of certain organisms take place in different habitats within an aquatic ecosystem. This phenomenon was described e.g. by Van der Velde and Brock (1980) for the fly *Notiphila brunnipes*. As an adult, this fly is dependent on the aerial parts of *Nuphar lutea* and *Nymphaea alba*, while the larvae grow up in the rhizosphere of *Nymphoides*, *Typha* and/or *Acorus*. Fish species of which the full-grown individuals occur predominantly in deeper open water sites may use a nymphaeid vegetation as a nursery ground. A diurnal rhythm in the migration of certain organisms between nymphaeid vegetation and surrounding habitats also exists. This phenomenon was described e.g. for large-bodied cladocerans by Timms and Moss (1984).

It can be concluded that waterlily beds are open systems. The quantitative aspects of import and export of organic matter, nutrients and organisms certainly is an important topic for further research. Den Hartog (1980) stated that, as a result of the external relations, homogeneous macrophyte communities that cover extended areas are not necessarily richer in species or

more characteristic than smaller stands in contact with a variety of other habitats.

Concluding remarks.

As is demonstrated in this thesis, and in the literature cited, aquatic macrophytes play important roles in their ecosystems. Shallow freshwater systems in The Netherlands are often the sinks of the intensively exploited terrestrial systems, and consequently the misuse of our landscape is usually observed first in aquatic habitats. Aquatic macrophyte communities are threatened by human activities, which result e.g. in unnatural water level fluctuations, and in eutrophication, acidification and poisoning of the surface water. Aquatic macrophytes and the nature of the associated communities can be used as indicators for water quality It is important to emphasize that the maintenance of the natural potential of our shallow fresh water ecosystems is the only guarantee for a multifunctional use of the surface water. As Francis Bacon said "We cannot command nature except by obeying her".

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References.

Allen, H.L., 1971. Primary productivity, chemo-organotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. Ecol. Monogr., 41:97-127.

Ankersmid, M. and Kwak, R., 1978. Produktie-onderzoek aan *Nymphaea alba* L. in de Oude Waal bij Nijmegen. Rapport no. 66, Laboratorium voor Aquatische Oecologie, KUN, 65 pp.

Bärlocher, F. and Kendrick, B., 1975. Leaf-conditioning by microorganisms. Oecologia (Berl.), 20:395-362.

Blindow, I., 1984. Interactions between submerged macrophytes, epiphyton and phytoplankton: a review. Report of the Institute of Limnology, University of Lund, Sweden, 67 pp

Brock, Th.C.M., 1975 De terrestrische fauna van de nymphaeide waterplanten, *Nuphar lutea* (L.)Sm., *Nymphaea alba* L. en *Nymphoides peltata* (Gmel)O.Kuntze, op de plas de Oude Waal in de Ooijpolder bij Nijmegen Rapport no. 20, Laboratorium voor Aquatische Oecologie, KUN, 79 pp.

Brock, Th.C.M. and Van der Velde, G., 1983. An autecological study on *Hydromyza livens* (Fabricius) (Diptera, Scatomyzidae), a fly associated with nymphaeid vegetation dominated by *Nuphar*. Tijdschr. Entomol., 126:59-90.

Carignan, R., 1982. An empirical model to estimate the relative importance of roots in phosphorus uptake by aquatic macrophytes. Can. J. Fish. Aquat. Sci., 39:243-247.

Clasquin, L. and Crul, M., 1982. Jaaronderzoek naar de relatie tussen waterplanten en abiotische milieufaktoren en nutriënten-budgettering van de verschillende kompartimenten in twee wielen. Rapport no. 145, Laboratorium voor Aquatische Oecologie, KUN, 55 pp.

Dacey, J.W.H., 1981. Pressurized ventilation in the yellow waterlily. Ecology, 62:1137-1147.

Dacey, J.W.H. and Klug, M.J., 1982. Ventilation by floating leaves in *Nuphar*. Am. J. Bot., 69:999-1003.

Dale, H.M. and Gillispie, T., 1976. The influence of floating vascular plants on the diurnal fluctuations of temperature near the water surface in early spring. Hydrobiologia, 49:245-256.

Dederen, L., Drossaert, B., Kaufholz, M. and Schueler, J., 1982. Een onderzoek naar de differentiatie van makro-evertebraten in door nymphaeiden gedomineerde systemen met een kritische beschouwing van de daarmee samenhangende minimumareaal bepalingen. Rapport no. 173, Laboratorium voor Aquatische Oecologie, KUN, 144 pp.

Delbecque, E.J.P., 1983. A comparison of the periphyton of *Nuphar lutea* and *Nymphaea alba*. The distribution of diatoms on the undersides of floating leaves. In: Wetzel, R.G. (ed.), Periphyton of freshwater ecosystems. Dr. W. Junk Publishers, The Hague, pp. 41-47.

Den Hartog, 1980. Structural and functional aspects of macrophyte-dominated aquatic systems. Proc. E.W.R.S. 5th Symp. on Aquatic Weeds, 1978.

Esteves, F., 1979. Die Bedeutung der aquatischen Makrophyten für den Stoffhaushalt des Schöhsees. II. Die organischen Haubtbestandteile und der Energiegehalt der aquatischen Makrophyten. Arch. Hydrobiol., Suppl. 57:144-187.

Gaevskaya, N.S., 1969. The role of higher aquatic plants in the nutrition of the animals of freshwater basins. Translation edited by K.H. Mann, National Lending Library for Science and Technology, Boston Spa, England, vol.1-3, 629 pp.

Geelen, J.F.M., Segers, P. and Suykerbuyk, R., 1980. Kwalitatief en kwantitatief planktononderzoek van de Bemmelse Strang en de Bizonbaai. Rapport no. 125, Laboratorium voor Aquatische Oecologie, KUN, 38 pp.

Heine, M. and Van der Velde, G., 1978. De muskusrat, *Ondatra zibethicus* (L.), in de Ooijpolder bij Nijmegen en zijn invloed op de nymphaeide vegetaties. De Levende Natuur, 81:122-128.

Jacobs, R.P.W.M., 1982. Pythiaceous fungi associated with the decomposition of *Nymphoides peltata*. Antonie van Leeuwenhoek, 48:433-445.

Kaul, V., 1971. Production and ecology of some macrophytes of Kashmir lakes. Hidrobiologia (Bucuresti), 12:63-69.

Kunii, H., 1983. Diurnal vertical fluctuations in some water variables under the covers of two different aquatic plants, *Elodea nuttallii* and *Trapa* sp.. Mem. Fac. Sci., Shimane Univ., 17:61-69.

Lammens, E.H.R.R. and Van der Velde, G., 1978. Observations on the decomposition of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae) with special regard to the leaves. Aquat. Bot., 4:331-346.

Leemans, H.B.J., 1980. Epifytische diatomeeën op *Nymphoides peltata* in de Bemmelse Strang. Rapport no. 121, Laboratorium voor Aquatische Oecologie, KUN, 45 pp.

Leuven, R.S.E.W. and Dederen, L.H.T., 1981. Een oriëntering op kwalitatieve en kwantitatieve methodieken bij macrofauna onderzoek, met speciale aandacht voor het nymphaeide systeem. Rapport no. 128, Laboratorium voor Aquatische Oecologie, KUN, 138 pp.

Makirinta, U., 1978. Spektrale Lichtmessungen im freien Wasser und in der Wasservegetation des Sees Kukkia, Südfinnland, unter besonderer Berücksichtigung der Zonation. Aquilo Ser. Bot., 16:39-53.

Marshall, E.J.P. and Westlake, D.F., 1978. Recent studies on the role of aquatic macrophytes in their ecosystem. Proc. EWRS 5th Symp. on Aquatic Weeds, 1978:43-51.

Pitlo, R.H., 1978. Regulation of aquatic vegetation by interception of daylight. Proc. EWRS 5th Symp. on Aquatic Weeds, 1978:91-99.

Pitlo, R.H., 1979. Biologisch slootonderhoud met behulp van drijvende vegetaties. Waterschapsbelangen, 13:283-290.

Roijackers, R.M M., 1983. Primary productivity of the phytoplankton in the Oude Waal near Nijmegen. A comparison between the nymphaeid dominated zone and the open water zone. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18-23 September, 1983 pp 203-207.

Roijackers, R.M.M., 1984. Some structural characteristics of the phytoplankton in the Oude Waal near Nijmegen, The Netherlands. Verh. Internat. Verein. Limnol , 22:1687-1694.

Sand-Jensen, K., Prahl, C. and Stokholm, H., 1982 Oxygen release from roots of submerged aquatic macrophytes. Oikos, 38:349-354.

Søndergaard, M., 1981. Kinetics of extracellular release of 14C-labelled organic carbon by submerged macrophytes. Oikos, 36:331-347.

Stemkens, T. and Meekes, H., 1978. Een onderzoek naar de rol van de bodem en de macrofyten in de nutrienten-cyclus en naar de biomassa van de macrofyten in de Oude Waal bij Nijmegen en het Haarsteegse Wiel bij Vlijmen. Rapport no. 100, Laboratorium voor Aquatische Oecologie, KUN, 61 pp.

Timms, R.M. and Moss, B., 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. Limnol. Oceanogr., 29:472-486.

Twilley, R.R., Brinson, M.M., and Davis, G.J., 1977. Phosphorus absorption, translocation, and secretion in *Nuphar luteum*. Limnol. Oceanogr., 22:1022-1032.

Van der Aa, H.A., 1978. A leaf spot disease of *Nymphaea alba* L. in the Netherlands. Neth. J. Pl. Path., 84:109-115.

Van der Velde, G., 1980. Studies in nymphaeid-dominated systems, with special emphasis on those dominated by *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae), Thesis Catholic University, Nijmegen, 163 pp.

Van der Velde, G. and Brock, Th.C.M., 1980. The life history and habits of *Notiphila brunnipes* Robineau-Desvoidy (Diptera, Ephydridae), an autecological study on a fly associated with nymphaeid vegetation. Tijdschr. Entomol., 123:105-127.

Van der Velde, G. and Hiddink, R., submitted. Chironomidae mining in *Nuphar lutea* (L.)Sm. (Nymphaeaceae). Ent. Scand., submitted.

Van der Velde, G. and Peelen-Bexkens, P.M.M., 1983. Production and biomass of floating leaves of three species of Nymphaeaceae in two Dutch waters. Proc. Int. Symp Aquat. Macrophytes, Nijmegen, 18-23 September, 1983:230-235.

Van der Velde, G. and Van der Heijden, L.A., 1981. The floral biology and seed production of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae). Aquat. Bot., 10:261-293.

Van der Velde, G. and Van der Heijden, L A., 1985. Initial decomposition of floating leaves of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae) in relation to their age, with special attention to the role of herbivores. Verh. Internat. Verein. Limnol., 22:2937-2941.

Van der Velde, G., Brock, Th C.M., Heine, M., and Peeters, P.M.P.M., 1978. Flowers of Dutch Nymphaeaceae as a habitat for insects. Acta Bot. Neerl., 27:429-438.

Van der Velde, G., Meuffels, H.J.G., Heine, M. and Peeters, P.M.P.M., accepted. Dolichopodidae (Diptera) of a nymphaeid-dominated system in The Netherlands: species composition, diversity, spatial and temporal distribution. Aquat. Insects, accepted.

Van der Velde, G., Van der Heijden, L.A., Van Grunsven, P.A.J. and Bexkens, P.M.M., 1982. Initial decomposition of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae), as studied by the leaf-marking method. Hydrobiol. Bull. (Amsterdam), 16:51-60.

Van Gool, P., 1982. Ostracoda van de Oude Waal en Bemmelse Strang. Rapport no. 154, Laboratorium voor Aquatische Oecologie, KUN, 24 pp.

Van Gool, P., Spies-van Rooyen, N. and Verhoeven-Boonstra, M., 1982. Kwalitatief en kwantitatief planktononderzoek van de Oude Waal en de Bemmelse Strang in 1981. Rapport no. 132, Laboratorium voor Aquatische Oecologie, KUN, 75 pp.

Vintges, V. and Verhoeven, F., 1977. Een onderzoek naar de produktie en afbraak van *Nuphar lutea* (L.)Sm. in de Oude Waal bij Nijmegen. Rapport no. 99, Laboratorium voor Aquatische Oecologie, KUN, 124 pp.

Wetzel, R.G., 1975. Limnology, W.B. Saunders, Philadelphia, 743 pp.

Wetzel, R.G. and Manny, B.A., 1972. Secretion of dissolved organic carbon and nitrogen by aquatic macrophytes. Verh. Int. Verein. Limnol., 18:162-170.

Willmer, P.G., 1982. Hygrothermal determinants of insect activity patterns: the Diptera of water-lily leaves. Ecol. Entomol., 7:221-231.

Zonderwijk, P. and Van Zon, J.C.J., 1976. Waterplanten als bondgenoten bij het onderhoud, Waterschapsbelangen, 61:21-23.

Inleiding.

Ondiepe zoete wateren zoals oude rivierlopen, vennen en sloten komen veelvuldig voor in het Nederlandse landschap. Hogere waterplanten kunnen in dergelijke systemen aspectbepalend zijn en een belangrijke oecologische betekenis hebben Alhoewel de afgelopen jaren veel informatie m.b.t. hogere waterplanten beschikbaar is gekomen, is de kennis van door deze planten gedomineerde zoetwatergemeenschappen fragmentarisch Biomassa, productie, decompositie, voedingsstoffenkringlopen en interacties tussen organismen zijn zelden diepgaand bestudeerd aan dezelfde waterplantengemeenschappen. Een min of meer compleet model van de structuur, functie en dynamiek van een aantal algemeen voorkomende waterplantengemeenschappen is echter belangrijk, zo niet onontbeerlijk, voor een adequaat beheer van de talrijke ondiepe wateren in Nederland.

Om deze redenen ging op het Laboratorium voor Aquatische Oecologie (Katholieke Universiteit, Nijmegen) in 1973 een onderzoeksproject van start m.b.t. de structuur, functie en dynamiek van door hogere planten gedomineerde aquatische systemen. In het zoete water concentreerde het onderzoek zich op gemeenschappen waarin nymphaeide waterplanten aspectbepalend zijn. Waterplanten met een nymphaeide groeivorm wortelen in de bodem, worden gekenmerkt door het bezit van opvallende drijfbladeren en van bloemen die op het water drijven of er bovenuit steken. Vegetaties gedomineerd door nymphaeiden zijn zeer algemeen en wijd verspreid in Nederland. De verschillende oecologische aspecten van dergelijke vegetaties zijn/worden door meerdere medewerkers van de afdeling Aquatische Oecologie onderzocht. Door integratie van de diverse deelstudies moet het mogelijk zijn om een min of meer compleet model omtrent de structuur, functie en dynamiek van gemeenschappen gedomineerd door nymphaeiden te verkrijgen. Het in dit proefschrift beschreven onderzoek is bedoeld als een bijdrage tot een beter inzicht in de overlevingsbiologie en oecologische betekenis van de nymphaeide waterplanten *Nymphoides peltata* (Watergentiaan), *Nuphar lutea* (Gele plomp) en *Nymphaea alba* (Waterlelie).

Watergentiaan

De Watergentiaan wordt over het algemeen aangetroffen in stilstaande of zwakstromende voedingsstoffenrijke wateren met een hoge alkaliniteit zoals sloten, oude rivierlopen en kleiafgravingen. De plant groeit bij voorkeur op een minerale bodem (vooral klei), al dan niet bedekt met een relatief dunne organische laag. Vooral wateren gelegen in de uiterwaarden, die in de winter of het vroege voorjaar door rivierwater overspoeld worden, zijn geschikte groeiplaatsen. Extreem hoge waterstanden in de zomer, die plotseling op kunnen treden als de rivieren buiten hun oevers treden, kan de Watergentiaan echter slecht verdragen. Het tijdelijk droogvallen van de standplaatsen in het groeiseizoen wordt goed getolereerd. De plant groeit optimaal bij een waterdiepte van 20-150 cm.

De Watergentiaan heeft een aantal typische pionierkenmerken zoals de capaciteit om zich zeer snel generatief en vegetatief te vermeerderen en een relatief korte levensduur van alle organen. Zelfs de ondergedoken plantedelen worden doorgaans niet ouder dan enkele jaren. De zaden kunnen lange droogteperiodes doorstaan en kiemen goed in vochtige drooggevallen milieus. Binnen een jaar kan uit een kiemplant een volgroeide plant met drijfbladeren ontstaan. Met behulp van over de bodem kruipende uitlopers kan de Watergentiaan binnen een relatief korte tijd een groot oppervlak van een geschikte groeiplaats in beslag nemen. Vergeleken met de Waterlelie en de Gele plomp is bij de Watergentiaan het aandeel van de ondergrondse biomassa, en dus de hoeveelheid reservestoffen, laag. De gedurende de afgelopen jaren waargenomen achteruitgang van de Watergentiaan in de uiterwaarden van de Waal kan mogelijk verklaard worden door de uitputting van de reservestoffen, als gevolg van de plotseling optredende extreem hoge waterstanden, gedurende het groeiseizoen van een aantal opeenvolgende jaren.

Gele plomp en Waterlelie.

De Gele plomp en Waterlelie kunnen in allerlei typen stilstaande en zwakstromende wateren tot een diepte van ca. 3 m gevonden worden. In hun gevestigde fase tolereren beide soorten dat het water verzuurt of wordt verrijkt met voedingsstoffen. In Nederland kunnen de Gele plomp en Waterlelie dan ook

aangetroffen worden in het traject van verzuurde voedselarme wateren tot en met gebufferde voedingsstoffenrijke systemen. Nietemin heeft de Gele plomp zijn optimum in meer gebufferde voedselrijke wateren, terwijl de Waterlelie vaker gevonden wordt in zachte, voedselarme systemen. Beide soorten groeien op allerlei minerale en organische bodems. Golfslag en bootverkeer kunnen het voorkomen van nymphaeiden beperken tot een relatief smalle zone nabij de oever. De Gele plomp echter verdraagt over het algemeen golfslag en waterbewegingen beter dan de Waterlelie. In de gevestigde fase kunnen deze planten extreem hoge waterstanden beter verdragen dan de Watergentiaan. Het tijdelijk droogvallen van de standplaatsen wordt eveneens goed getolereerd door de volgroeide planten.

De volgroeide planten van de Gele plomp en de Waterlelie bezitten in de regel een goed ontwikkeld wortelstelsel. In de wortelstokken van deze planten kunnen grote hoeveelheden reservestoffen opgeslagen zijn. Deze worden benut voor de ontwikkeling van het bladerdek in het voorjaar of na ernstige beschadigingen van de bladeren tijdens het groeiseizoen. Hierdoor kan verklaard worden waarom de Gele plomp en Waterlelie tijdens het groeiseizoen kort durende maar extreem hoge waterstanden (waardoor veel bladeren afsterven) kunnen overleven. In vergelijking met de Watergentiaan investeren de Gele plomp en de Waterlelie meer in de opbouw van een reservestoffen-voorraad en minder in een snelle vegetatieve uitbreiding. De laatstgenoemde twee soorten bezitten geen uitlopers en de levensduur van hun wortelstokken kan oplopen tot verscheidene decennia. Alhoewel beide soorten de capaciteit hebben om vele zaden te produceren, worden zelden kiemplanten gevonden in wateren waar wel volgroeide planten te vinden zijn. De voorwaarden en condities voor een succesvolle zaadkieming en vestiging van de kiemplanten in het veld zijn nog grotendeels onbekend en momenteel onderwerp van een ander promotieonderzoek.

De oecologische betekenis.

Productie.

De bovengrondse biomassa van de Watergentiaan, Waterlelie en Gele plomp is meestal niet hoger dan ca. 300-350 g asvrij-drooggewicht per m^2. Hun totale biomassa kan echter veel hoger zijn dankzij een goed ontwikkeld wortelstelsel. In de

Oude Waal werd bij de Waterlelie een maximale biomassa van meer dan 1 kg asvrij drooggewicht per m^2 aangetroffen.

Alhoewel de bovengrondse biomassa van de Watergentiaan, Waterlelie en Gele plomp relatief laag is kan de jaarlijkse productie van organisch materiaal door de bovengrondse delen van deze planten oplopen tot ca. 970 g asvrij-drooggewicht per m^2. Door hun hoge productiecapaciteit spelen deze nymphaeiden een belangrijke rol in de voedselketens en bij de ophoping van organisch materiaal. Vooral de bladeren dragen bij tot het grootste deel van de jaarlijkse productie. De gemiddelde levensduur van de bladeren van bovengenoemde nymphaeiden is in de regel vrij kort en varieert bijvoorbeeld in oude rivierlopen van 18-46 dagen. Gedurende het gehele groeiseizoen worden nieuwe bladeren geproduceerd om oude te vervangen. Hierdoor is de toevoer van organisch materiaal naar de omgeving een min of meer constant proces gedurende het groeiseizoen.

Decompositie.

Maar een relatief klein deel (minder dan 10%) van de jaarlijkse productie van nymphaeide waterplanten wordt door herbivore dieren geconsumeerd. Het overgrote deel van de jaarlijkse productie sterft af en verdwijnt in de detritus voedselketen. Door de beschadigingen die herbivoren aanrichten kan de levensduur van de bladeren echter aanzienlijk verkort worden.

Tijdens de afbraak van het plantenmateriaal lekken allerlei oplosbare bestanddelen uit en worden organische verbindingen gemineraliseerd door micro-organismen. In gebufferd, voedselrijk water is het aandeel van bacteriën bij de afbraak van Watergentiaan-bladeren groter dan dat van schimmels. De afbraaksnelheid van plantenmateriaal is afhankelijk van de structuur en chemische samenstelling van dat materiaal. Zo vertonen de verschillende organen van nymphaeiden over het algemeen verschillen in afbraaksnelheid; de bovengrondse organen kenmerken zich door een snellere fragmentatie en gewichtsverlies dan de ondergrondse delen. Ook bestaan er soortsspecifieke verschillen in afbraaksnelheid. Na het afstervingsproces en onder vergelijkbare milieu-omstandigheden breken de bladeren van de Watergentiaan sneller af dan die van de Waterlelie, terwijl de drijfbladeren van de Gele plomp nog langzamer afbreken. In vergelijking met vele andere oever- en waterplanten echter, vertonen bovengenoemde nymphaeiden een relatief snelle

decompositie. Dit verschijnsel hangt samen met de relatief lage hoeveelheden cellulose, hemicellulose en lignine in de bovengrondse delen van de Watergentiaan, Waterlelie en Gele plomp.

De activiteit van micro-organismen, en dus de afbraak van organisch materiaal, is in hoge mate afhankelijk van externe milieuomstandigheden zoals de temperatuur, de zuurgraad, alkaliniteit en voedingsstoffengehalte van het omringende water. In zure niet gebufferde wateren is de afbraaksnelheid laag en accumuleren structurele koolhydraten (vooral hemicellulose) in het resterende plantenmateriaal. In gebufferde en/of voedselrijke systemen is de afbraaksnelheid hoog en accumuleert vooral lignine, terwijl cellulose en hemicellulose relatief snel verdwijnen. De moeilijk afbreekbare fracties hopen zich op in de bodem waardoor na verloop van tijd ondiepe wateren kunnen verlanden.

Kringloop van mineralen.

Voor een optimale groei hebben planten voldoende voedingszouten nodig zoals stikstof en fosfor. De Watergentiaan, Gele plomp en Waterlelie nemen stikstof en fosfor actief op en wel in die mate dat de concentraties van deze elementen in de plantenweefsels vaak vele malen hoger zijn dan die van hun directe omgeving. Deze planten kunnen zelfs meer stikstof en fosfor opnemen dan strikt noodzakelijk is voor hun groei. Nymphaeide waterplanten hebben de waterkolom en het sediment als voedingsstoffenbron ter beschikking. In ondiepe wateren is de bovenste bodemlaag over het algemeen het grootste reservoir van stikstof en fosfor. Hier kan men vaak meer dan 95% van de totaal in het systeem aanwezige stikstof en fosfor vinden. Het grootste deel hiervan is echter niet direct voor nymphaeide waterplanten beschikbaar, daar deze elementen op complexe wijze gebonden kunnen zijn aan bodemdeeltjes. Desalnietemin zijn de concentraties aan opneembare stikstof en fosfor in het bodemwater in de regel vele malen hoger dan die in de waterkolom. Voor nymphaeide waterplanten is dan ook de bodem de belangrijkste stikstof- en fosforbron. De via de wortels opgenomen voedingsstoffen worden voor een groot deel vastgelegd in de bovengrondse biomassa. Ten tijde van de maximale biomassa kunnen nymphaeide waterplanten een relatief groot gedeelte van de beschikbare hoeveelheden stikstof en fosfor vastgelegd hebben. Tijdens de afbraak van vooral de bovengrondse

plantendelen kunnen de voedingsstoffen vrijkomen in het water of gedeeltelijk, gebonden aan rottend plantenmateriaal, naar de bodem verdwijnen. Aldus kunnen nymphaeide waterplanten in ondiepe wateren als voedingsstoffenpomp fungeren, waardoor oorspronkelijk in de bodem aanwezige mineralen in de waterkolom vrijkomen. Deze mineralen kunnen door algen in het perifyton en het plankton benut worden.

Andere invloeden op fysisch-chemische omgevingsfactoren.

Dichte begroeiingen van nymphaeide waterplanten beinvloeden waterbewegingen. Drijfbladeren dempen de golfslag en de waterverplaatsing onder het drijfbladdek wordt tot op zekere hoogte belemmerd door de bladstelen en ondergedoken bladeren. Nymphaeide waterplanten nemen overigens maar een relatief klein deel van de waterkolom in beslag waardoor de doorstromingsweerstand bij deze planten over het algemeen geringer is dan bij dichte begroeiingen van de meeste ondergedoken waterplanten. Het temperen van waterbewegingen kan leiden tot een gelaagdheid van de temperatuur en zuurstofconcentratie in de waterkolom. De wortels van de Watergentiaan, Waterlelie en Gele plomp kunnen verhinderen dat het sediment weggespoeld wordt. Deze invloeden van nymphaeide waterplanten op het temperen van waterbewegingen en de stabilisatie van de bodem kunnen bijdragen tot een heldere waterkolom en zijn voor veel op en tussen de vegetatie levende organismen gunstig.

Bij ondergedoken waterplanten kunnen processen zoals fotosynthese en respiratie voor dagelijkse fluctuaties in de pH en de concentraties van zuurstof en anorganische koolstof in de waterkolom zorgen. In vegetaties met volgroeide nymphaeiden is dit in mindere mate het geval daar koolzuurgas en zuurstof bij nymphaeiden voornamelijk rechtstreeks worden uitgewisseld met de atmosfeer. Nymphaeide waterplanten hebben zelfs een overwegend negatief effect op de zuurstofbalans van het water daar de uitwisseling van zuurstof tussen lucht en water verminderd wordt door de drijfbladeren en omdat tijdens de afbraak van de bladeren zuurstof uit de waterkolom wordt verbruikt. Nietemin is de zuurstofconcentratie van het water onder een drijfbladdek meestal hoog genoeg voor dierlijk leven daar algen het water van zuurstof voorzien en zuurstofrijk water relatief gemakkelijk getransporteerd wordt naar nymphaeide vegetaties.

Nymphaeide waterplanten beïnvloeden in sterke mate het lichtklimaat van de waterkolom omdat de drijfbladeren een groot deel van het licht onderscheppen. Door beschaduwing van de waterkolom kunnen de Watergentiaan, Waterlelie en Gele plomp een uitbundige groei van ondergedoken waterplanten temperen en wordt de groei van algen beïnvloed. Doordat bepaalde dieren in het beschaduwde water minder opvallend zijn kunnen nymphaeide vegetaties dienst doen als schuilplaats voor dieren waarop door bijvoorbeeld watervogels en vissen gejaagd wordt.

Nymphaeide waterplanten beïnvloeden de omgevingstemperatuur. Een deel van het invallende licht wordt namelijk omgezet in warmte aan het oppervlak van planten. De temperaturen van de bloemen en de bovenzijde van de drijfbladeren kunnen tot 5°C hoger worden dan de omringende lucht. Hierdoor wordt de transpiratie door deze waterplanten verhoogd en is gedurende de dag de luchtvochtigheid boven drijfbladeren doorgaans iets hoger dan boven een vrij wateroppervlak. In vegetaties met nymphaeiden kan de temperatuur van de bovenste centimeters van de waterkolom verscheidene graden hoger worden dan op plaatsen zonder hogere planten. De diepere waterlagen onder een drijfbladdek kunnen echter tijdens zonnige dagen koeler blijven dan op vegetatieloze plaatsen. De beïnvloeding van de omgevingstemperatuur door nymphaeide waterplanten heeft uiteraard gevolgen voor de activiteiten van andere organismen.

Betekenis voor andere organismen.

Mede door de typische architectuur van nymphaeide waterplanten en de specifieke fysisch-chemische condities in hun nabijheid kunnen allerlei organismen deze planten voor verschillende doeleinden benutten. De bloemen van de Watergentiaan, Gele plomp en Waterlelie worden bezocht door gevleugelde insecten (o.a. de Aardhommel, de Honingbij en verscheidene zweefvliegen) die er nectar, pollenkorrels en/of stempelvocht verzamelen. De meeste van deze insecten zijn typische landdieren en voor de voltooiing van hun levenscyclus niet afhankelijk van nymphaeide waterplanten. De vlieg *Notiphila brunnipes* echter is wat de voedselvoorziening betreft voor een groot deel aangewezen op de bloemen van de Waterlelie en Gele plomp. Deze vlieg kan men dan ook als een kensoort van het nymphaeide systeem beschouwen.

Alhoewel slechts een klein deel van de jaarlijkse productie van nymphaeide waterplanten door begrazing verdwijnt, spelen deze planten toch een belangrijke rol als directe voedselbron voor verscheidene dieren. De levende plantenweefsels kunnen geconsumeerd worden door enkele watervogels (o.a. Meerkoet en Smient), de Muskusrat, koeien en verscheidene insecten en slakken. Een aantal herbivore insecten zoals de kevers *Donacia crassipes* en *Pyrrhalta nymphaeae* f. *typica*, de vliegelarve *Hydromyza livens* en de muggelarve *Endochironomus lepidus* zijn voor de voltooiing van hun levenscyclus afhankelijk van nymphaeide waterplanten. Overigens kunnen de herbivoren van deze waterplanten meestal niet gerekend worden tot de typische waterfauna (organismen die hun gehele levenscyclus in het water volbrengen). Dit verschijnsel zou verklaard kunnen worden door het feit dat hogere planten in een vrij laat stadium van de evolutie het zoete water gekoloniseerd hebben, terwijl de typische waterfauna, meer gespecialiseerd in het eten van algen en detritus, zich toen al ontwikkeld had.

Het afgestorven plantenmateriaal van de Watergentiaan, Gele plomp en Waterlelie is een zeer belangrijke voedsel- en energiebron voor micro-organismen. Het complex van afgestorven plantenmateriaal, bacterien en schimmels kan een zeer geschikt substraat zijn voor allerlei detritivore dieren, die zich o.a. met de aanwezige micro-organismen voeden. De detritivoren zijn weer een geschikt voedsel voor dieren met een carnivore levenswijze. Per gram (asvrij-drooggewicht) detritus van nymphaeide waterplanten kan men onder bepaalde omstandigheden tot ca. 800 individuen van macro-evertebraten aantreffen.

Nymphaeide waterplanten kunnen door talrijke zoetwaterorganismen als een geschikte aanhechtingsplaats benut worden. Bij dichte begroeiingen van deze planten kan de hoeveelheid plantenoppervlak dat benut wordt door waterorganismen oplopen tot tot ca. 6 m^2 per m^2 systeem. In Nederlandse wateren is het oppervlak van waterplanten vaak het enige vaste substraat van betekenis dat beschikbaar is voor bepaalde algen en verscheidene diergroepen. De organismen die vastgehecht zitten aan waterplanten rekent men tot het perifyton. Het perifyton van nymphaeide waterplanten wordt vaak gekenmerkt door kiezelwieren. Dit kan te wijten zijn aan de korte levensduur van de bladeren en/of de geringe lichtintensiteit onder het drijfbladdek. De algen van het perifyton zijn een uitstekend voedsel voor allerlei meer

beweeglijke dieren zoals slakken, muggelarven en kokerjuffers. Ook kunnen minder mobiele dieren die voedsel uit het omringende water filtreren nymphaeide waterplanten als aanhechtingsplaats gebruiken.

De drijfbladeren van nymphaeide waterplanten spelen een zeer belangrijke rol als paarplaats en eiafzetplaats voor allerlei dieren. Voor de typische waterfauna zijn de drijfbladeren als eiafzetplaats gunstig omdat het omringende water hier relatief zuurstofrijk en warm is. Ook zijn de bladeren als eiafzetplaats gemakkelijk te bereiken voor allerlei gevleugelde insecten die in hun volwassen stadium op het droge vertoeven maar waarvan de larven in het water leven. De volgroeide larven van dergelijke dieren (o.a. libellen en schietmotten) gebruiken de drijfbladeren vaak ook voor hun gedaanteverwisseling.

Naast bovengenoemde functies kunnen nymphaeide waterplanten een belangrijke rol spelen als leverancier van voedingszouten (o.a. voor algen) en zuurstof (o.a. voor minerende en bodembewonende insecten), als jachtterrein voor zowel land- (o.a. vogels) als waterdieren (o.a. vissen), als schuil- en rustplaats en als bouwmateriaal.

Vanwege de vele functies die nymphaeide waterplanten kunnen vervullen voor andere organismen kan men doorgaans een groter aantal soorten en individuen van organismen in nymphaeide vegetaties vinden dan op vergelijkbare plaatsen zonder waterplanten. In de Bemmelse Strang, een oude rivierloop nabij Nijmegen, werden tussen en op de Watergentiaan 459 verschillende soorten algen en aquatische evertebraten aangetroffen, terwijl in het open water slechts 284 soorten gevonden werden. De meeste algen en waterdieren die gevonden kunnen worden op nymphaeide waterplanten zijn niet typisch voor het nymphaeide systeem op zich daar ze ook op andere typen waterplanten gevonden kunnen worden. Een tiental soorten insecten, met zowel aanpassingen aan lucht als water, is min of meer typisch voor het nymphaeide systeem.

Ik hoop met bovenstaande verhandeling over nymphaeide waterplanten duidelijk gemaakt te hebben dat waterplanten in ondiepe wateren belangrijke functies kunnen vervullen. Het is daarom zeer de moeite waard om de talrijke ondiepe wateren van Nederland, waarin waterplanten aspectbepalend zijn, goed te beheren. Dit geldt zowel voor de relatief zeldzame ondiepe wateren zoals duinplassen als voor het gewone slootmilieu. Het behoud van de natuurlijke potentie van ondiepe wateren is

uiteindelijk de enige waarborg voor een veelzijdig gebruik van het oppervlaktewater door de mens.

CURRICULUM VITAE

Theodorus Cornelis Maria Brock, roepnaam Theo, werd op 23 augustus 1953 geboren te Goirle. Op 10 juni 1970 behaalde hij zijn diploma mulo-A en -B aan de St. Radboudschool voor U.L.O. te Oldenzaal. Op 28 juni 1972 werd de havo-opleiding met succes afgesloten aan de Pedagogische Academie, Oude Dijk, te Tilburg. In hetzelfde jaar begon hij zijn studie m.o. plant- en dierkunde aan de Katholieke Universiteit, Nijmegen. Op 6 september 1977 werd hier zijn akte van bekwaamheid tot het geven van middelbaar onderwijs in de plant- en dierkunde behaald, tesamen met het kandidaatsexamen biologie (Blg). Tijdens de doctoraalperiode van de studie biologie had hij het voorrecht om twee hoofdvakstudies te verrichten. In het kader van het hoofdvak Aquatische Oecologie, onder begeleiding van Dr. G. van der Velde, werd onderzoek verricht naar de bloembiologie van nymphaeide waterplanten en naar de levenswijze van een aantal karakteristieke insecten van het nymphaeide systeem. Gedurende het hoofdvak Geobotanie, onder begeleiding van Prof. Dr. V. Westhoff, werden in 1976 en in 1978 vegetatiekundige studies verricht aan de westkust van de Republiek Ierland. Aldaar werden de vegetaties van duinen, duingraslanden, kwelders, moerassen en plassen van de "Dooaghtry area" beschreven. Het bijvak Didactiek van de Biologie betekende voor hem een oriëntatie op verschillende didactische werkvormen, waaronder projectonderwijs. Het doctoraalexamen werd (cum laude) afgelegd op 5 juni 1979. Tevens behaalde hij nogmaals zijn onderwijsbevoegdheid. Op 16 augustus 1979 werd hij benoemd tot wetenschappelijk medewerker in tijdelijke dienst bij het Laboratorium voor Aquatische Oecologie van de Katholieke Universiteit, Nijmegen. Onder leiding van Prof. Dr. C. den Hartog en Dr. G. van der Velde werd een promotieonderzoek verricht naar de oecologie van nymphaeide waterplanten. Dit onderzoek werd op 15 augustus 1984 afgesloten. Gedurende de contractperiode begeleide hij drie maal de jaarlijkse cursus Mariene Biologie voor post-kandidaten van de afdeling Aquatische Oecologie en de Terschelling-week van de cursus Aquatische Oecologie voor derde jaars biologie-studenten. Een groot deel van de resultaten van het promotieonderzoek is het afgelopen jaar uitgewerkt tot een proefschrift.

Beckers, A., Brock, Th. & Klerkx, J., 1976. A vegetation study of some parts of Dooaghtry, Co. Mayo, Republic of Ireland. Report of the Laboratory for Geobotany, Catholic University, Nijmegen, 76 pp.

Brock, Th.C.M., 1975. De terrestrische fauna van de nymphaeide waterplanten, *Nuphar lutea* (L.)Sm., *Nymphaea alba* L. en *Nymphoides peltata* (Gmel.)O Kuntze, op de plas de Oude Waal in de Ooijpolder bij Nijmegen. Rapport no. 20, Laboratorium voor Aquatische Oecologie, Katholieke Universiteit, Nijmegen, 79 pp.

Brock, Th.C.M., 1981. Nitrogen and phosphorus budgets of a nymphaeid-dominated system. Hydrobiol. Bull. (Amsterdam), 15· 191-192.

Brock, Th., 1982. De landschappelijke en biologische waarde van sloten. Zuidhollands landschap 4('82): 12-15.

Brock, Th.C.M., 1983. The distribution of elements in a *Nymphoides peltata*-dominated system. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18-23 September, pp. 41-45.

Brock, Th.C.M., 1984. Aspects of the decomposition of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae). Aquat. Bot., 19: 131-156.

Brock, Th.C.M., 1985. De invloed van oever- en waterplanten op hun omgeving, met speciale aandacht voor fysisch-chemische factoren. 33ste Heterosis-Cursus 1984-1985 (Wageningen, 9-1-1985), 6 pp.

Brock, Th.C.M., 1985. Verspreiding en oecologische betekenis van de Watergentiaan (*Nymphoides peltata* (Gmel.)O.Kuntze). Mededelingen W.A.P., 7. 1-8.

Brock, Th.C.M., 1985. Aspects of production and decomposition of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae). Verh. Internat. Verein. Limnol., 22: (in press).

Brock, Th.C.M., 1985. Remarks on the distribution and survival biology of the White, Yellow and Fringed waterlily: an introduction. In: Th.C.M. Brock, Ecological studies on nymphaeid water plants. Thesis, Catholic University, Nijmegen, 204 pp.

Brock, Th.C.M., 1985. The ecological role of the White, Yellow and Fringed waterlily: a synthesis. In: Th.C.M. Brock, Ecological studies on nymphaeid water plants. Thesis, Catholic University, Nijmegen, 204 pp.

Brock, Th.C.M., Arts, G.H.P., Goossen, I.L.M. & Rutenfrans, A.H.M., 1983. Structure and annual biomass production of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae). Aquat. Bot., 17: 167-188.

Brock, Th.C.M., Bongaerts, M.C.M., Heijnen, G.J.M.A. & Heijthuijzen, J.H.F.G., 1983. Nitrogen and phosphorus accumulation and cycling by *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae). Aquat. Bot., 17: 189-214.

Brock, Th.C.M., Boon, J.J. & Paffen, G.P., 1985. The effects of the season and of water chemistry on the decomposition of *Nymphaea alba* L.: weight loss and pyrolysis mass spectrometry of the particulate matter. Aquat. Bot. 22: 197-229.

Brock, Th.C.M., De Lyon, M.J.H., Van Laar, E.M.J.M. & Van Loon, E.M.M., 1985. Field studies on the breakdown of *Nuphar lutea* (L.)Sm. (Nymphaeaceae), and a comparison of three mathematical models for organic weight loss. Aquat. Bot., 21: 1-22.

Brock, Th., Frigge, P. & Van der Ster, H., 1978. A vegetation study of the pools and surrounding wetlands in the Dooaghtry area, Co. Mayo, Republic of Ireland. Report of the Laboratory for Geobotany, Catholic University, Nijmegen, 155 pp.

Brock, Th.C.M., Huijbregts, C.A.M., Van der Steeg-Huberts, M.J.H.A. & Vlassak, M.A., 1982. In situ studies on the breakdown of *Nymphoides peltata* (Gmel.)O.Kuntze (Menyanthaceae): some methodological aspects of the litter bag technique. Hydrobiol. Bull. (Amsterdam), 16: 35-49.

Brock, Th. & Leuven, R., 1983. Onderhoud van sloten. Zuidhollands landschap, 3 ('83): 16-19.

Brock, Th., Van Campen, L. & Edlinger, B., 1980. Een oriéntatie op de functie, biologie en beheer van sloten in Nederland. Scriptie no. 14, Laboratorium voor Aquatische Oecologie, Katholieke Universiteit, Nijmegen, 78 pp.

Brock, Th.C.M. & Van der Velde, G., 1983. An autecological study on *Hydromyza livens* (Fabricius) (Diptera, Scatomyzidae), a fly associated with nymphaeid vegetation dominated by *Nuphar*. Tijdschr. Ent., 126: 59-90.

Brock, Th.C.M., Van der Velde, G. & Van de Steeg, H.M., accepted. The effects of extreme water level fluctuations on the wetland vegetation of a nymphaeid-dominated oxbow lake in the Netherlands. Arch. Hydrobiol. Suppl. (accepted).

De Lyon, M.J H., Van Laar, E.M.J.M. & Brock, Th.C.M., 1983. A comparison of three mathematical models for the description of breakdown of *Nuphar lutea*-detritus. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18-23 September 1983, pp. 129-133.

Leuven, R.S.E.W., Brock, Th.C.M. & Van Druten, H.A.M., 1985. Effects of preservation on dry- and ash-free dry weight biomass of some common aquatic macro-invertebrates. Hydrobiologia, 127: 151-159.

Leuven, R.S.E.W., Den Hartog, C., Geelen, J.F.M. & Brock, Th.C.M., 1984. Effecten van zure neerslag op de waterkwaliteit, flora en fauna van zwak gebufferde wateren in Nederland In: Adema, E.H. & Van Ham, J. (Eds), Zure regen: oorzaken, effecten en beleid. Pudoc, Wageningen, pp 134-140.

Paffen, B.G.P. & Brock, Th.C.M., 1984. In situ and in vitro studies on the breakdown of *Nymphaea alba* L. (Nymphaeaceae). Hydrobiol. Bull. (Amsterdam), 18: 72-73.

Van der Velde, G. & Brock, Th.C.M., 1980. The life history and habits of *Notiphila brunnipes* R.-D. (Diptera, Ephydridae), an autecological study on a fly associated with nymphaeid vegetation. Tijdschr. Ent., 123: 105-127.

Van der Velde, G., Brock, Th.C.M., Heine, H. & Peeters, P.M.P.M., 1978. Flowers of Dutch Nymphaeaceae as a habitat for insects. Acta Bot. Neerl., 27: 429-430.

STELLINGEN

I

De huidige verspreiding van de Gele plomp en de Waterlelie in ondiepe wateren in Nederland is niet zozeer het gevolg van de momenteel aanwezige fysische en chemische factoren, maar veeleer van in het verleden heersende milieu-omstandigheden.

II

Extreem hoge waterstanden van de Waal gedurende de zomer, zoals die vooral de laatste jaren waargenomen zijn, vinden hun oorzaak in cultuur-technische ingrepen in het afwateringsgebied van de boven- en middenloop van de Rijn, en vormen een bedreiging voor de natuurwaarden van ondiepe wateren in de uiterwaarden.

Brock, van der Velde & van de Steeg.
Arch. Hydrobiol. Suppl. (accepted).

III

De gangbare methode bij decompositie-experimenten in het water om plantenmateriaal te drogen alvorens het te incuberen, beïnvloedt de initiële afbraak in hoge mate. Deze methode is dus verwerpelijk.

Brock, Huijbregts, Van der Steeg-Huberts & Vlassak (1982).
Hydrobiol. Bull., 16: 35-49.

IV

Indien de zure neerslag kan worden teruggedrongen, vereist de restauratie van cultureel verzuurde ondiepe wateren een verwijdering van de bovenste bodemlaag.

V

Bij het mechanisch onderhoud van watergangen is tot nu toe nauwelijks onderzoek verricht naar het effect van de frequentie en het tijdstip van onderhoud op de (her)groei van waterplanten.

VI

De indeling van de biologie-opleiding te Nijmegen in een fysiologisch-biochemische richting (in de wandelgangen research richting) en een algemeen-oecologische richting geschiedt te vroegtijdig en is bovendien kunstmatig.

VII

Alhoewel kleine, ondiepe wateren zeer karakteristiek voor Nederland zijn en onderzoek hieraan beslist niet bodem- en oeverloos genoemd kan worden, bestaat er bij BION werkgemeenschappen weinig interesse voor levensgemeenschappen van dergelijke systemen.

VIII

Dat wetenschappers van de Katholieke Universiteit Nijmegen bij wetenschappelijke publicaties wel de universiteit van Nijmegen vermelden, maar vaak de katholieke signatuur verzwijgen, kan te maken hebben met opportunisme of met een minderwaardigheidscomplex.

IX

De kunde van het doceren gaat gepaard met de kunst van het doseren.

X

Dat super-gespecialiseerde organismen vaak kwetsbaar zijn voor veranderende omstandigheden kan als waarschuwing gelden voor de beoefenaars van wetenschap.

Stellingen behorende bij het proefschrift van Theo Brock, "Ecological studies on nymphaeid water plants".

Nijmegen, 4 december 1985.